EVOLUTION OF THE TAPIROID SKELETON FROM *HEPTODON* TO *TAPIRUS*

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INTRODUCTION

The purpose of this study is two-fold: first, to describe and illustrate the best-pre-served known skeleton of an early Eocene perissodactyl and, second, to investigate the morphological changes which occurred during about 50 million years of evolution from the late early Eocene tapiroid *Hepto-don* to the recent genus *Tapirus*.

Although equoid and tapiroid remains are fairly common in early Eocene deposits, good skeletons of these or other early Eo-cene perissodactyls are discouragingly rare. Most of the skeletal elements which have been found are incomplete, crushed, or coated with a hard deposit which makes preparation difficult. For these reasons no well-documented description of the osteol-ogy of an early Eocene perissodactyl has heretofore been published. The most de-tailed previous study, Kitts' revision of *Hyracotherium* (1956), is inadequately il-lustrated. The present paper therefore should fill a critical gap in knowledge of perissodactyl evolution.

This study is based on an almost com-plete, well preserved, and excellently pre-pared skeleton of *Heptodon posticus*, an early Eocene helaletid tapiroid. All early Eocene perissodactyls appear to have been

extremely similar in skeletal morphology, with the main differences between the major groups expressed in the dentition. The osteological differences which do exist apparently reflect relatively small differ-ences in size and do not appear to have phylogenetic significance. Therefore, the skeleton of *Heptodon* described below rep-resents, probably fairly closely, the ancestral morphology not only of all later tapiroids, but of all other perissodactyls as well. To facilitate future studies by workers to whom the original material is not readily available, the bones described here are illustrated with figures drawn from several views.

Heptodon probably was directly ancestral to the modern tapirs, as well as to several extinct tapiroid lineages (see Radinsky, 1963a). In the following description com-parisons are made between the skeleton of *Heptodon* and that of a modern species of *Tapirus*, *T. pinchaque*, to determine the ex-tent of the osteological changes which oc-curred in this most conservative of surviving perissodactyl lineages. To aid interpreta-tion of the functional significance of the observed changes, reference was made to Bressou, 1961, and to Campbell, 1936 and 1945, the most recent accounts of the myol-ogy of Recent species of *Tapirus*. In addi-tion, I dissected the facial and fore limb musculature of a specimen of *Tapirus indi-cus*. My own observations and the pub-lished accounts confirm Gregory's (1929) restoration of the relatively unspecialized

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musculature of a titanothere. Gregory's work is still the best one to consult for illustrations of muscle origins and insertions on the perissodactyl skeleton.

The skeleton of *Heptodon posticus* here described, MCZ 17670,[2] was collected in Lostcabinian (late Wasatchian) beds in the Wind River basin, Wyoming, by Mr. Henry Seton, who published a preliminary note on the specimen in 1931. Mr. Seton has generously allowed me to complete the description. The scientific value of MCZ 17670 has been greatly enhanced by Seton's skill and painstaking work in preparing it. Postcranial remains of *Heptodon* are known in only one other specimen, AMNH 294, an incomplete skeleton of *H. calciculus*. This was briefly described by Osborn and Wortman (1892), and differs from *H. posticus* primarily in its smaller size and more slender build. The systematics of *Heptodon* have been discussed in a recent revision of North American tapiroids (Radinsky, 1963a).

Of the four living species of *Tapirus*, *T. pinchaque* was chosen for comparison with *Heptodon* mainly because it is the least specialized of the surviving tapirs, and also because it is the rarest and least well known of the four species. Illustrations of its postcranial skeleton are published for the first time in this paper. Specimens of *Tapirus pinchaque* examined for this study include: MCZ:M 6037, YPM 204, and AMNH:M 149331 and 149424.

For knowledge of intermediate stages between *Heptodon* and *Tapirus*, comparisons were made with *Protapirus*, a primitive Oligocene tapirid. Although known species of *Protapirus* occur too late in time to be directly ancestral to later tapirids (see Schaub, 1928, p. 13), the genus is probably

representative of a morphological stage through which the main line of tapirid evolution passed. Of the skeleton of *Protapirus*, only the skull, atlas, fore limb (PU 10899), and manus (AMNH 662) are known. These were originally described by Hatcher (1896), and Wortman and Earle (1893), respectively, and were most recently redescribed by Scott (1941).

To avoid repetition in the comparisons of bones of *Heptodon* and *Tapirus*, differences in size will not be mentioned. These may be calculated from the illustrations. It will suffice to note here that *Heptodon posticus* is about 40 per cent smaller than *Tapirus pinchaque*.

OSTEOLOGY

Skull and Mandible

The skull of *Heptodon posticus* included in MCZ 17670 is one of the best-preserved early Eocene perissodactyl skulls ever discovered (see Pls. 1–3). A slight anterior displacement of the right side of the skull, and a crushing of the right side of the rostrum, which resulted in a slight dorsal displacement of the right nasal bone, are the only evident distortions in proportions.

[2] Abbreviations of institutions are: AMNH, the American Museum of Natural History, Department of Vertebrate Paleontology; AMNH:M, same, Department of Mammalogy; MCZ, Museum of Comparative Zoology, Division of Vertebrate Paleontology; MCZ:M, same, Division of Mammalogy; PU, Princeton University; YPM, Yale Peabody Museum.
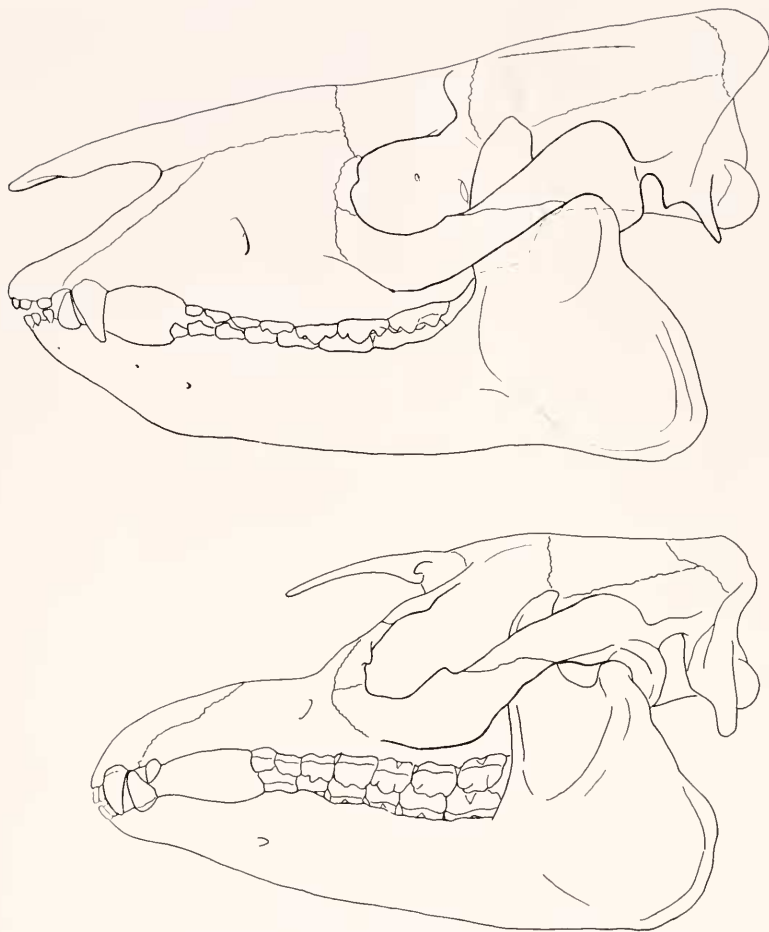
Fig. 1. Skull and mandible. Above, *Heptodon posticus*, MCZ 17670, × ½. Below, *Tapirus pinchaque*, YPM 204 (after Hatcher, 1896, pl. 5), × ¼.

The skull (see Fig. 1 and Pls. 1–3) is relatively long and narrow, measuring 195 mm from the anterior tip of the premaxilla to the dorsal edge of the foramen magnum, and about 80 mm wide across the zygomatic arches. The occiput is 56 mm high (from basioccipital to top of nuchal crest) and has a maximum width of 46 mm (across the post-tympanic processes). The preorbital portion of the skull is slightly longer than the postorbital portion. The nasal incision extends back to a point over the postcanine diastema, closer to P^1 than C^1. The premaxillae contact the nasals dorsally and ex-clude the maxillae from the nasal incision. The infraorbital foramen is located above the front of P^3 and the anterior edge of the orbit is above the anterior border of M^2. The lacrimal has a relatively small facial portion, and bears a triangular tubercle on the rim of the orbit. The supraorbital processes are relatively massive and are followed by a pronounced postorbital constriction. The braincase is slightly expanded and the sagittal and lambdoidal crests are prominent. The zygomatic arches are relatively slender. The external auditory meatus is widely open ventrally; it is bounded ante-

riorly by a relatively prominent postglenoid process and posteriorly by a short, antero-ventrally projecting post-tympanic process. The paroccipital process is relatively long and thin, slightly flattened anteroposteriorly, and extends posteroventrally and slightly laterally.

The palate is almost flat from front to back and only slightly arched transversely. It has a pair of small elongate incisive foramina between the third incisors, and a long deep anterior median groove which may have opened into the nasal passage. The internal nares open at the posterior border of M^2. The interpterygoid fossa is relatively deep and narrow, with no trace of a vomer on the presphenoid almost as far forward as the anterior border of the choanae. The glenoid fossa is relatively flat. It is bounded posteriorly by a strong post-

glenoid process which is oriented postero-laterally at an angle of about 30 degrees from the long axis of the skull. The basi-cranial axis is inclined slightly anterodor-sally relative to the plane of the palate.

At the anterior edge of the orbit (see Fig. 2) the lacrimal bone is too broken to allow accurate determination of the number or configuration of the openings into the nasolacrimal canal. The maxillary foramen is visible in the extreme anteroventral corner of the orbit. The sphenopalatine foramen is located above the anterior edge of M^3, and is relatively large; a small posterior palatine foramen is located posteroventral to the sphenopalatine foramen. Sutures between the bones of the orbit cannot be definitely determined, partly due to the advanced age of MCZ 17670 (the teeth are heavily worn), and partly because the bones are extensively fractured.

The posterior part of the medial wall of the orbit (see Fig. 2) is pierced by four foramina, arranged in a posteroventrally descending row. Beginning with the most anterior one, which is located a short distance behind the posterior palatine foramen, these are: a small ethmoid foramen, a very large optic foramen, a smaller, vertically-bilobed, slit-like, anterior lacerate foramen (= orbital fissure or sphenoidal foramen), and the anterior opening of the alisphenoid canal. Examination of the interior of the braincase revealed a small foramen, apparently the foramen rotundum, opening into the alisphenoid canal. The optic foramen is unusually large and Simpson (1952, p. 200) suggested that the equally large, apparently homologous foramen in *Hyracotherium* was the confluent opening of the optic and anterior lacerate foramina. However, inside the braincase of *Heptodon* it can be seen that the left and right internal openings of the large foramen in question are confined entirely within the bounds of the optic chiasma and there are no grooves suggesting that nerves other than the optic left through the foramen. The presence of
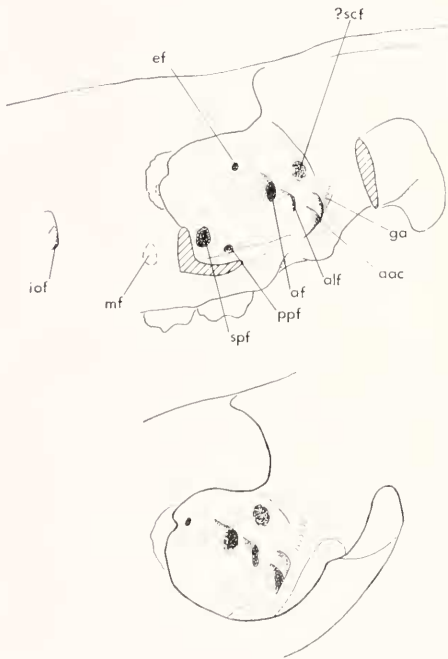

Fig. 2. *Heptodon posticus.* MCZ 17670. Above, lateral view of orbital region with zygomatic arch removed. Below, anterolateral view of same region. × ½. For abbreviations see p. 102.

a foramen opening into the alisphenoid canal confirms the interpretation that the slit-like opening behind the optic foramen is the anterior lacerate foramen.

Above and slightly posterior to the anterior lacerate foramen on each side of the skull is an irregularly-shaped opening, at least part of which is artificial, but which may include a natural opening into the braincase (presumably the sinus canal foramen). There is a pit immediately above the anterior opening of the alisphenoid canal. A shallow vertical groove which ascends

Fig. 3. *Heptodon posticus.* MCZ 17670. Left, restoration of basicranial region of skull. Right, ventrolateral view of restored left petrosal, with tympanic and tegmen tympani removed. × ½.

from the laterodorsal border of the anterior opening of the alisphenoid canal may mark the course of the supraorbital artery, or possibly the deep temporal artery.

The foramen ovale (see Fig. 3) is separated from the middle lacerate foramen by a strip of alisphenoid about 7.5 mm wide,

the posterior border of which is notched by two grooves. The more lateral of the two, located just medial to the anterior edge of the postglenoid process, is relatively broad and probably marks the passage of the internal maxillary artery. The second, more medial groove, is narrow and slit-like, and probably contained the chorda tympani. The postglenoid foramen is relatively large. In ventral view the basisphenoid overlaps the ventral border of the petrosal. There is a medium-sized posterior lacerate foramen, a relatively large hypoglossal (or condyloid) foramen, and a medium-sized mastoid foramen.

Both petrosals of MCZ 17670 lack small portions, but fortunately the missing parts of each petrosal are preserved on the opposite side so that it is possible to obtain a composite picture of the entire bone (see Fig. 3). The ventral border of the petrosal is relatively long and convex, and the anterior border is relatively short and concave. Seen in ventrolateral view, the surface of the petrosal is flat anteroventrally, and swells posterodorsally towards a relatively low promontorium. The surface of the promontorium is smooth, and shows no traces of grooves for blood vessels. The tegmen tympani extends relatively far ventrally, forming the lateral wall of a deep groove for the facial nerve. This is similar to the condition in modern tapirs in which the facial nerve runs posteriorly along the lateral face of the petrosal in a ventrally-open groove, rather than in an enclosed canal. Two small foramina are present on the lateral face of the tegmen tympani. The lower and slightly more medial one probably is the facial hiatus, and thus served for the exit of the great superficial petrosal nerve (which joins the great deep petrosal nerve anteriorly to form the vidian nerve). The higher and more laterally situated foramen may have transmitted the small superficial petrosal nerve.

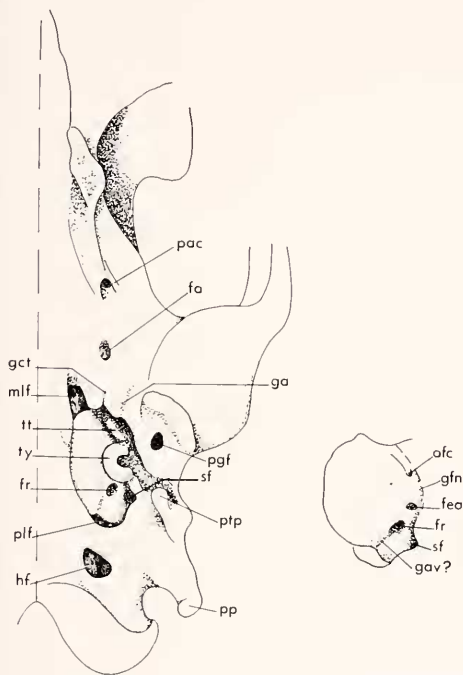The tegmen tympani is broken off above the level of the facial canal on the right

petrosal, exposing the opening of the facial canal and the fenestra ovalis. The latter is located posteriorly and slightly ventrally from the former. A very small foramen, possibly a nutrient foramen, is present on both petrosals a short distance anteroventral to the fenestra ovalis. The fenestra rotunda is located a short distance posteroventral to the fenestra ovalis. A deep V-shaped groove extends posteroventrally from the fenestra rotunda and separates the main body of the petrosal from a small, globose posterior portion. This groove occupies approximately the same position as the auricular branch of the vagus nerve (which joins the facial nerve near the stylomastoid foramen), but appears too large to have housed that nerve alone.

The stylomastoid foramen is represented by a broadly open groove anteromedial to the post-tympanic process. No tympanohyal is preserved; the broken surface anterior to the stylomastoid foramen on left and right petrosals suggests that one may originally have been present. There are no separate fossae for the stapedius or tensor tympani muscles. These presumably occupied the same groove as the facial nerve, the tensor tympani at the anterior end of the groove, lateral to the facial nerve, and the stapedius at the posterior end, medial to the nerve.

On the medial side of the petrosal a shallow depression adjacent to the concavity of the anterior edge may have accommodated the semilunar (Gasserian) ganglion of the trigeminal nerve. The internal auditory meatus is relatively large and elongate in an almost vertical direction. Cochlear and vestibular aqueducts are visible near the posterior edge of the petrosal, the former posteroventral and the latter posterodorsal to the internal auditory meatus.

The entire tympanic bone was preserved on the left side but was largely destroyed during the preparation of a latex mold of the skull. Fortunately, photographs and drawings made by Henry Seton prior to this mishap provide a record of the configuration of this bone. The tympanic in this early Eocene tapiroid is a semicircular strip of bone, dorsoventrally flattened and slightly expanded in a horizontal plane. In other words, it is only slightly modified from the simple, narrow, open tympanic ring which is considered primitive for mammals. Kitts (1956, p. 17) stated that the early Eocene equoid *Hyracotherium* had a tympanic bulla which was ". . . apparently oval in shape and moderately inflated." Re-examination of the specimens involved showed that Kitts mistook the petrosal for a tympanic bulla. Except for the skull of *Heptodon posticus* described here, I know of no other specimen of an early Eocene perissodactyl in which the tympanic is preserved. The tympanic probably was a relatively narrow semicircular strip of bone in all early Eocene perissodactyls. Its failure to be preserved in otherwise complete skulls is probably because it was loosely attached to the skull, as in modern tapirs.

Portions of at least some of the auditory ossicles are visible dorsal and medial to the tympanic ring, but are too fragile to be removed from the last remnants of the hard sandstone matrix. Their description must await discovery of additional specimens.

The symphysis is slightly constricted and extends back as far as P_1. Its dorsal surface is deeply concave transversely. Three small mental foramina are visible, beneath C_1, the middle of the diastema, and P_2. The body of the mandible is relatively long and slender, with a very slightly convex ventral border. The angle is moderately convex and extends relatively far behind the condyle and slightly below the ventral border of the body. The condyle is located relatively high above the tooth row and is inclined medioventrally at an angle of about 20 degrees from horizontal. Its articular surface slopes anteriorly and a small facet continues ventrally onto the medial third of the posterior face of the condyle. The coronoid process is relatively small and vertical. On the lateral surface of the ascending

ramus a pronounced fossa for the zygomaticomandibularis extends ventrally to about the level of the tooth row. The border of the insertion area of the masseter is marked by a fairly prominent ridge for most of its length. The medial surface of the angle is slightly concave and bears prominent scars from the insertion of the internal pterygoid.

COMPARISON WITH TAPIRUS

The skull of *Tapirus pinchaque* (see Fig. 1) differs from that of *Heptodon* in several features, most of which are related to one or more of three basic developments: evolution of a proboscis, relative enlargement and change in proportions of the brain, and increased specialization of the masticatory apparatus.

The most obvious differences between the skulls of *Heptodon* and *Tapirus* are those associated with proboscis development. Primary modifications for the proboscis are the enlargement (or retraction) of the nasal incision, which provides room for the main mass of the proboscis, and shortening of the nasals, to allow flexibility to that organ. The nasal incision in *Tapirus* extends back over the orbits, and the nasals do not reach beyond the first premolar. An additional factor which adds to the vertical dimension of the nasal incision in *Tapirus* is the higher position of the nasals in that genus, which results from the presence of a frontal sinus. Frontal sinus development is correlated with changes in brain proportions, and will be discussed below. The nasal diverticulum (a blind cartilaginous sac which opens into the main nasal passage) has been displaced from the nasal incision in *Tapirus* and is lodged in a long, broad groove which begins on the ascending process of the maxilla, extends up along the posterior border of the incision on the anterior edge of the frontals, and terminates in a curl on the posterior edge of the nasals. The absence of a groove or fossa for the nasal diverticulum in *Heptodon* indicates that the diverticulum in that primitive ta-

piroid must have been relatively small and lodged in the nasal incision, as in modern horses and rhinos.

Secondary cranial modifications associated with proboscis development in *Tapirus* include a posterior displacement of the nasal cavity, strengthening of the premaxillae, and possibly the anterior shift of the orbit. In *Heptodon* the nasal cavity is located in front of the orbit, with the cribriform plate situated near the anterior border of the frontals, at the anterior edge of the orbit. In *Tapirus*, the tremendous expansion of the nasal incision has removed most of the lateral walls of the rostrum, and the greater part of the chamber which houses the ethmoturbinals is located *between* the orbits, with the cribriform plate located well behind the orbit, near the posterior border of the frontals. This has resulted in a lateral displacement of the walls of the orbit which obliterates the postorbital constriction and greatly deaccentuates the supraorbital processes. Another result of the posterior displacement of the nasal chamber relative to the orbits is that the internal nares, which open posteriorly in *Heptodon*, open downward as well as backward in *Tapirus*.

The expansion of the nasal incision in *Tapirus* has left the premaxillae extending far out, relatively unsupported. Presumably to strengthen this area against the vertical stresses which result from use of the incisors, the premaxillae are thickened and arch downward and, with the anterior ends of the maxillae, are closer together, forming a relatively deep, narrow, and arched projection on which the incisors and canines are borne. Associated with this development, the two lateral incisive foramina seen in *Heptodon* are merged into a single, large, median opening in *Tapirus*, extending back almost to the first premolar. The large size of this opening is probably related to the fact that it occupies that part of the palate least involved in transmitting vertical stresses from the incisors and canines, and

thus needs no bony support. Another factor possibly related to the strengthening of the premaxillae in *Tapirus* is the large size of the third incisor, which has been transformed into a small tusk which occludes against the front of the large lower canine. The upper third incisor of *Tapirus* is located more anteriorly than its functional counterpart, the upper canine, is in *Heptodon*, and would require stronger premaxillae for support.

The orbit is located more anteriorly in *Tapirus* than in *Heptodon*. This may be advantageous for operation of the proboscis since the main muscles involved (the levator nasolabialis and superior and inferior maxillolabialis) take origin on the anterior rim of the orbit and it would be mechanically more advantageous to have them originate nearer to their insertions. Another result of the anterior displacement of the orbit in *Tapirus* is that it brings the masseter forward over a greater portion of the tooth row, which increases the mechanical advantage of that muscle in mastication (see discussion below).

The skull is larger and heavier relative to the body in the modern tapir than in *Heptodon*. Probably reflecting this difference, the paroccipital process is relatively more robust, and is vertically oriented and fused to the post-tympanic process, and the back of the skull is relatively wider, suggesting relatively stronger neck muscles in *Tapirus* than in *Heptodon* (see p. 81). However, stronger cervical musculature might also be correlated with increased stresses resulting from the use of the proboscis. Another factor which may be pertinent here is orientation of the head. In *Heptodon* the occlusal plane diverges anteroventrally from the basicranial axis, while in *Tapirus* the occlusal plane is parallel or slightly anterodorsally inclined to the basicranium. This suggests that the head is held slightly more horizontally in *Tapirus* than it was in *Heptodon*, possibly in response to its relatively

heavier weight, or possibly because of the proboscis.

A second major factor which has been responsible for differences between the skulls of *Heptodon* and *Tapirus* is brain evolution. Evolution of the tapiroid brain will be described in a future paper. For the present discussion it will be sufficient to note that in tapiroids, as in equoids, a major feature of brain evolution (described in a classic work by Edinger, 1948) has been the expansion of the cerebral hemispheres and relative decrease in size of the olfactory bulbs. In *Heptodon*, the olfactory bulbs are relatively long, underlying most of the length of the frontals, and lie at the same level dorsally as the cerebrum. In *Tapirus*, the olfactory bulbs are relatively short, lying under only about the posterior third of the frontals, and the dorsal surface of the olfactory bulb chambers is at a lower level than that of the expanded cerebrum. The anterior part of the frontals is underlain by the posteroventrally-sloping nasal chamber. Since the ventral surface of the frontals immediately overlies the olfactory bulbs, and the dorsal surface must remain high to keep the nasal incision open, the external and internal tabulae of the frontal bone in *Tapirus* have become separated by a space, the frontal sinus. Thus, formation of the frontal sinus in *Tapirus* may be thought of as a response to the necessity of maintaining the nasals high above the orbits (to provide room for the proboscis beneath) when growth of the olfactory bulbs failed to keep pace with cerebral expansion and growth of the rest of the skull. (For a more thorough discussion of frontal sinus formation, see Edinger, 1950.)

As a direct result of cerebral expansion, the braincase of *Tapirus* is relatively wider than that of *Heptodon*. Sagittal and lambdoidal crests are relatively lower and do not project back as far in *Tapirus* as in *Heptodon*, perhaps because the expanded braincase provides more room for attachment of the temporal muscles in the modern form.

Or, on the other hand, the lower crests may reflect a relatively smaller amount of temporal musculature in *Tapirus*. The prominent sagittal and lambdoidal crests on the skull of *Heptodon* create a dorsal profile which diverges posterodorsally from the basicranial axis and occlusal plane. In *Tapirus pinchaque* the weaker crests and expanded frontal sinus result in a dorsal skull profile which parallels the basicranial axis.

The foramen ovale and postglenoid foramen have shifted posteriorly in *Tapirus* and are confluent with the foramen lacerum medium. Edinger and Kitts (1954) have pointed out that similar shifts in the position of the foramen ovale have occurred in equoids and rhinocerotoids. These changes may be related to the cerebral expansion that occurred in all three groups, but the exact reasons are still obscure.

The third major area in which changes have occurred during evolution of the skull from *Heptodon* to *Tapirus* involves the masticatory apparatus. The molar cusp pattern of *Tapirus* is similar to that of *Heptodon*, differing only in the following features: metacone more labially located, providing a slightly longer metaloph; ectoloph shorter (posterior to metacone apex) and relatively less prominent; paralophid and metalophid virtually nonexistent; M_3 hypoconulid absent. In *Heptodon*, molar shear occurs between the lingual side of the ectoloph and labial side of the paralophid and metalophid, as well as between upper and lower cross-lophs. As a result of the differences noted above, molar shear in *Tapirus* is almost entirely confined to the cross-lophs, with the anterior sides of protoloph and metaloph above shearing against the posterior sides of protolophid and hypolophid below. The functional advantage or adaptive significance of eliminating ectoloph shear and emphasizing cross-loph shear is not immediately apparent. This trend occurred in other tapiroid families besides the Tapiridae (Helaletidae and Deperetellidae) while in still other tapiroid families (Lophi-odontidae and Lophialetidae) ectoloph shear was retained, or even emphasized.

Probably the most important change from the dentition of *Heptodon* to that of *Tapirus* has been the molarization of the premolars. In *Heptodon* none of the premolars are molariform; in *Tapirus*, P^1 and P_2 are submolariform and the remaining premolars are molariform. As a result, the cheek tooth row is relatively longer and there is a relatively larger surface area available for mastication in *Tapirus* than in *Heptodon*. Perhaps in response to this increase in occlusal area at the front of the tooth row, the anterior border of the origin of the masseter (marked by a scar on the maxilla and malar below the orbit) has shifted forward relative to the tooth row, and is located above the anterior border of M^1 in *Tapirus*, compared with about the middle of M^2 in *Heptodon*. This increases the mechanical advantage of the masseter by lengthening its lever arm (distance from the masseter to jaw articulation) relative to the lever arm of the resistance (distance from teeth to articulation). The orbit also is located relatively more anteriorly in *Tapirus* than in *Heptodon*, and the anterior edge of the masseter scar is in the same position relative to orbit in both forms. Since the anterior part of the masseter takes origin from the bones forming the lateroventral border of the orbit, it is possible that the selective advantages resulting from a forward shift of the masseter were a significant factor in bringing about the change in position of the orbit. However, it should be kept in mind that in horses and other mammals the anterior origin of the masseter has moved forward independent of the orbit, by shifting onto the maxilla anterior to the orbit, and also that there are other functional advantages (related to proboscis development) involved in an anterior shift of the orbit.

Another change in dentition between *Heptodon* and *Tapirus* has been the atrophy of the upper canine and enlargement and caninization of the upper third incisor.

Thus, in *Tapirus*, the upper third incisor has replaced the canine functionally, and the upper tusk occludes in front of the lower, the reverse of the usual mammalian condition. This may be related to proboscis development if, with the proboscis extending in front of the premaxilla, the upper canine is located too far back to be effective. Another consideration is that the atrophy of the upper canine increases the amount of space available in the diastema for manipulation of food. Even without this additional space, the postcanine diastema is relatively longer in *Tapirus* than in *Heptodon*.

Finally, there are several features, in which the skull of *Tapirus* differs from that of *Heptodon*, which do not seem to be correlated with the three major developments discussed above. The optic foramen is smaller relative to the size of the skull and the other orbital foramina in *Tapirus* than in *Heptodon*. The tympanic, a simple half-ring in *Heptodon*, is expanded anteroventrally and laterally and forms a short floor to the external auditory meatus in *Tapirus*, although it is never large enough to form an inflated auditory bulla. The petrosal of *Tapirus* differs from that of *Heptodon* in having a shallower subarcuate fossa, a tegmen tympani composed of cancellous rather than solid bone, and in having a tympanohyal fused to it.

The mandible of *Tapirus* is fairly similar to that of *Heptodon*, differing from the latter in having a more procumbent symphysis (in correlation with the downcurved premaxillae), a posteriorly curved coronoid process (which may increase the mechanical efficiency of the temporalis), a slightly more rounded angle, and a relatively shorter and wider condyle.

SKULL EVOLUTION

The few known skulls of fossil tapiroids reveal some of the intermediate stages in the evolutionary developments discussed above and provide information on the rates at which the changes took place.

In a late early Eocene specimen of *Heptodon calciculus* (AMNH 294), the nasal incision extends back to a point over P^1, and the premaxillae no longer contact the nasals. In the middle Eocene genus *Helaletes*, which may have included species near the ancestry of the Tapiridae, the nasal incision is tremendously enlarged, both dorsoventrally and posteriorly, and extends back as far as P^3. The anterior wall of the orbit is over M^1, and there is a groove for the nasal diverticulum on the ascending process of the maxilla. However, the nasals of *Helaletes* are unshortened and extend as far forward as the anterior border of the premaxillae. This suggests that *Helaletes* did not have a prehensile proboscis, since the long nasals would have restricted its mobility.

The next stage in cranial evolution in the line leading to modern tapirs is represented by the latest Eocene or early Oligocene species *Colodon? hancocki* (known from a few specimens in collections of the University of Oregon Museum of Natural History). In *Colodon? hancocki* the nasal incision is extended slightly more posteriorly than in *Helaletes*, but is not quite as deep posteroventrally. However, the nasals are shorter in *C.? hancocki*, extending only to to a point over the postcanine diastema. This suggests that by the beginning of the Oligocene ancestral tapirids had a proboscis which, judging from the degree of retraction of the nasal incision and nasal shortening, may have been almost as long as that of modern tapirs.

A North American late Oligocene skull of *Protapirus* (PU 10899), the most primitive known tapirid, was described and figured by Hatcher (1896). Scott (1941, p. 754 and pl. 79) provided a few additional observations and new illustrations, with the premaxillae, which are missing in the Princeton skull, restored from a second skull (South Dakota School of Mines 2829). Modifications for the proboscis in the late Oligocene *Protapirus* skull are in about the same stage of development as in *Colodon?*
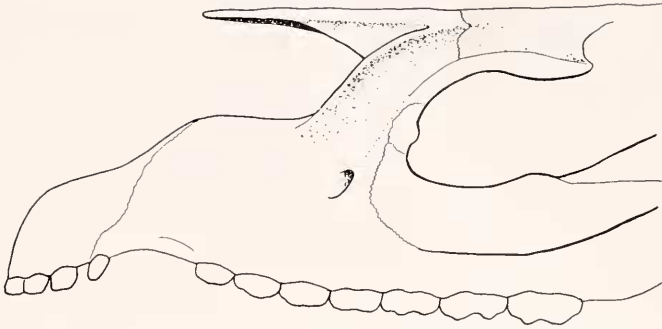
Fig. 4. *Protapirus.* Restoration of anterior half of skull, based mainly on PU 10899. Compare with Fig. 1. × ½.

hancocki. The nasal incision extends back to a point over P⁴, and the anterior edge of the orbit is over the middle of M¹. The nasals terminate slightly anterior to P¹. A broad groove for the nasal diverticulum extends up the ascending process of the maxilla, arches posteriorly into the dorsal surface of the prominent supraorbital process of the frontal, and continues back to the posterior border of the supraorbital process. This is a marked difference from the condition in *Tapirus*, where the supraorbital processes are suppressed and the groove for the nasal diverticulum curls medially and anteriorly to terminate on the posterior border of the nasals.

Both Hatcher's and Scott's illustrations of the Princeton *Protapirus* skull (drawn from the left side) show a deep groove on the anterior portion of the maxilla, parallel to the groove for the nasal diverticulum and separated from it by a high ridge. Examination of the right side of the skull shows that this anterior groove is an artifact, due to a break and inward crushing of the anterior part of the left maxilla. A new restoration of the anterior half of the skull of *Protapirus* is shown in Figure 4.

The nasal incision is narrower in *Protapirus* than in *Tapirus* because the anterior part of the maxilla is higher (less excavated) and the nasals are lower in the Oligocene genus. Scott (*loc. cit.*) considered the differences between the two forms great enough to suggest that in *Protapirus* the proboscis was only in an incipient stage. However, in Scott's restoration the nasal incision is drawn too narrow. In my opinion the nasal incision is large enough and the nasals are short enough in *Protapirus* to suggest that it had a fairly versatile proboscis.

There is still a marked postorbital constriction and the supraorbital processes are prominent in *Protapirus*, indicating that the nasal chamber did not extend back between the orbits in that genus. The premaxillae arch downwards, as in *Tapirus*, although the upper third incisor is not enlarged. The upper canine, however, is about as small as in the modern tapir. This indicates that the third incisor was enlarged after the atrophy of the canine, probably to functionally replace the upper canine in shear against the lower canine. The premolars are still nonmolariform to submolariform in *Protapirus*. The foramen ovale and postglenoid foramen are confluent with the foramen lacerum medium in *Protapirus*.

Although *Protapirus* possesses all the features one would expect to find in the ancestor of *Tapirus*, the known species of *Protapirus* appear too late in time to be directly ancestral to modern tapirs. Schuab (1928) described under the name *Tapirus helvetius* the anterior half of an almost modern tapirid skull from Europe, which he considered on the basis of lithological correlation to be of middle or late Oligocene age. Cranial

modifications for the proboscis are more advanced in *Tapirus helvetius* than in *Protapirus* in the following features: the nasal incision extends more posteriorly, reaching to a point over the orbit; the anterior part of the maxilla is lower and the nasals appear to be located slightly higher, leaving a deeper nasal incision; The groove for the nasal diverticulum curls onto the posterior border of the nasals, as in modern tapirs; the supraorbital processes are less pronounced. The anterior part of the skull of *Tapirus helvetius* is basically like that of *Tapirus pinchaque*, differing only in the following features: the nasal incision is not quite as deep posteroventrally, partly because a long posterior process of the premaxilla extends back over the maxilla to a point above the posterior edge of P^4; the nasals appear to be located slightly lower in the Oligocene species. Thus on the basis of anterior cranial morphology, *Tapirus helvetius* is intermediate between *Protapirus* and modern tapirs, but definitely closer to the latter. The same is true for its dentition— the premolars of *T. helvetius* are almost, but not quite, molariform.

Another tapirid close in age and similar in morphology to *Tapirus helvetius* was described by Schlaikjer (1937) under the name *Miotapirus harrisonensis*. This form, known only from the anterior half of a skull and a few limb bones (MCZ 2949) from early Miocene deposits in Wyoming, displays proboscis modification about as in *Tapirus helvetius*, except that the posterior process of the premaxilla is shorter, extending back to a point above P^2, and the nasals appear to be slightly higher. The skulls of *Tapirus helvetius* and *Miotapirus harrisonensis* indicate that by about the end of the Oligocene, or over 25 million years ago, cranial modifications for the tapirid proboscis were in essentially the same stage as in the recent species *Tapirus pinchaque*.

One of the major steps in the evolution of the proboscis was the tremendous enlargement of the nasal incision that occurred during the relatively short period of time between early Eocene *Heptodon* and middle Eocene *Helaletes*. Since the nasals were unshortened in *Helaletes* it seems unlikely that it had a proboscis; this suggests that the reasons for the initial enlargement of the nasal incision were probably not related to proboscis development. Primitively in perissodactyls the nasal diverticulum is lodged in the nasal incision. Enlarged nasal diverticula apparently have created depressions in the maxillary walls (preorbital fossae) and caused enlarged nasal incisions in many extinct perissodactyls (see Gregory, 1920). It therefore seems possible that expansion of the nasal diverticulum may have been responsible for the enlargement of the nasal incision in *Helaletes*. With the nasal incision enlarged, tapiroids would then have been preadapted for proboscis development.

Hyoid arch: Fragments of the hyoid arch are preserved in MCZ 17670, but most of the elements are too incomplete to yield much information. Neither ceratohyals nor thyrohyals were fused to the basihyal in *Heptodon*, and there is a long, low, irregular lingual process on the basihyal. In *Tapirus*, the thyrohyals are fused to the basihyal, and there is no lingual process.

AXIAL SKELETON

Vertebrae (Fig. 5): The vertebrae known for *Heptodon* include all the cervicals (except the fifth), the first two thoracic, and the last lumbar. In the atlas, the vertebrarterial canal enters at the posterior edge of the transverse process and emerges a short distance anteriorly on the ventral side. The atlantal (or alar) groove is open, notching the anterior edge of the transverse process. The neural spine of the last lumbar vertebra is only very slightly cranially inclined, which suggests reduced mobility of the vertebral column (Slijper, 1946, p. 103).

Vertebrae of *Tapirus* differ from those of *Heptodon* in the following features: cervical vertebrae relatively shorter and wider, with
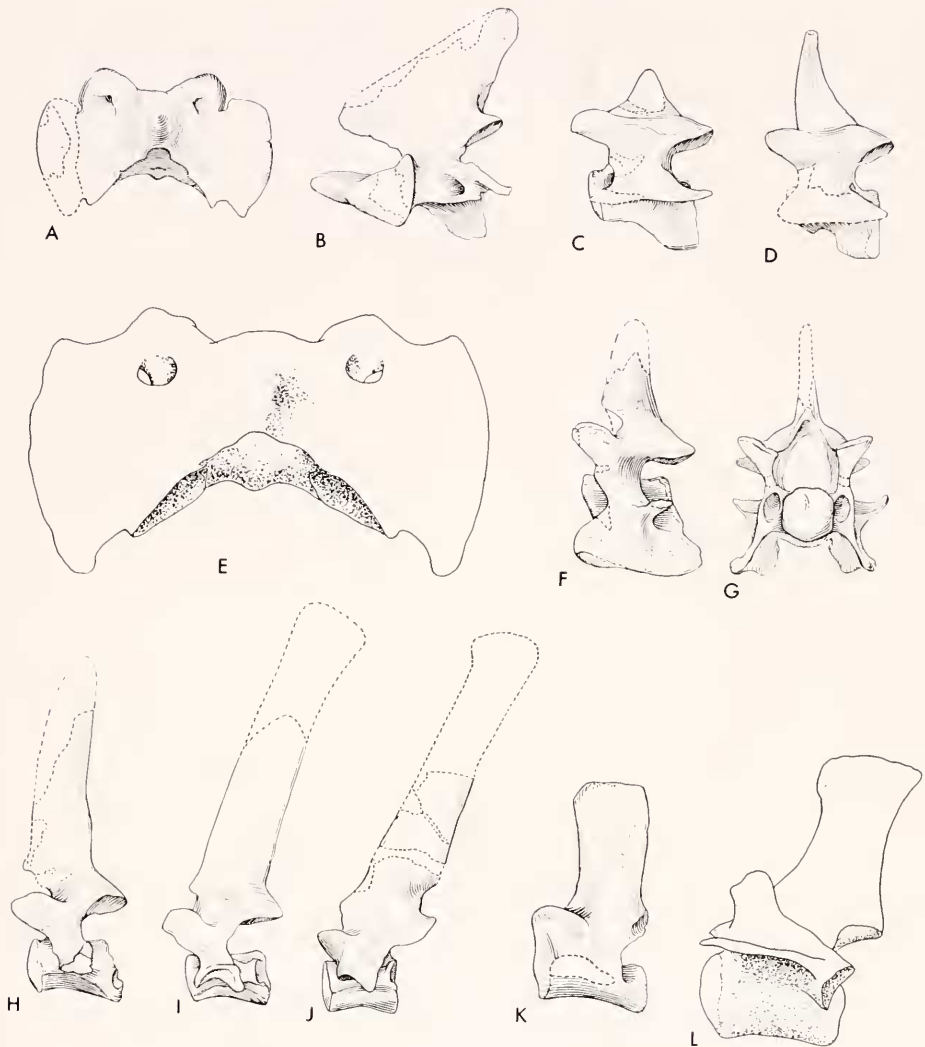
Fig. 5. Vertebrae of *Heptodon posticus* (MCZ 17670) and *Tapirus pinchaque* (AMNH:M 149424). A, E, dorsal views of atlases of *H. posticus* and *T. pinchaque*, respectively. B, C, D, lateral views of axis and third and fourth cervical vertebrae of *H. posticus*. F, G, lateral and anterior views of sixth cervical vertebra of *H. posticus*. H, I, J, lateral views of seventh cervical and first and second thoracic vertebrae of *H. posticus*. K, L, lateral views of last lumbar vertebra of *H. posticus* and *T. pinchaque*, respectively. All × ½.

anterior ends of centra more convex and posterior ends more deeply concave; atlantal groove of atlas bridged over by anterior growth of transverse process; odontoid process of axis relatively shorter and broader; neural spine of fourth cervical vertebra lower; postzygapophyses of first thoracic vertebra facing more laterally (and less

ventrally); neural spine of last lumbar vertebra slightly caudally inclined.

The shorter, wider and more opisthocoelous cervical vertebrae of *Tapirus* indicate a more powerful neck in the modern tapir than in *Heptodon*, probably in response to the needs of supporting a relatively larger and heavier head. The atlantal groove of

the atlas is bridged over in all modern perissodactyls and may simply reflect expansion of transverse processes to provide greater area for muscle attachment. The more laterally-facing postzygapophyses of the first thoracic vertebra restrict lateral movement but strengthen articulation between it and the following vertebra. The trend from cranial to caudal inclination of lumbar neural spines is correlated with decreasing importance of the longissimus muscles as spinal flexors and a backwards shift in their insertion from lumbar to sacral vertebrae. This results in decreased mobility of the vertebral column and is often correlated with increasing body weight (Slijper, 1946, pp. 103–104).

APPENDICULAR SKELETON

Scapula (Fig. 6): Only the glenoid end of the scapula is known for *Heptodon* but a fairly accurate restoration of the entire bone may be made by extrapolating from complete scapulae known for the early Eocene equoid *Hyracotherium* (figured in Kitts, 1956, pl. 2, fig. 1) and the middle Eocene tapiroid *Helaletes* (several specimens in collections of the United States National Museum). The posterior border is straight, the vertebral border straight to gently convex, and the anterior border more strongly convex. The neck is moderately constricted. The spine extends ventrally almost to the glenoid and is high at its ventral border. It has a small tuber spinae and a relatively prominent acromion. Infraspinatus and supraspinatus fossae are about equal in area. The tuber scapulae is low and bears a small coracoid process.

In *Tapirus* the spine is reduced ventrally, terminating more dorsally than in *Heptodon*, and bears no acromion. The ventral reduction of the spine accentuates the prominence of the tuber spinae. There is no projecting coracoid process and the tuber scapulae is considerably higher and more prominent, and forms the ventral border

Fig. 6. Right scapula. Left, *Heptodon posticus*, hypothetical restoration, × ½. Right, *Tapirus pinchaque*, MCZ:M 6037, × ¼.
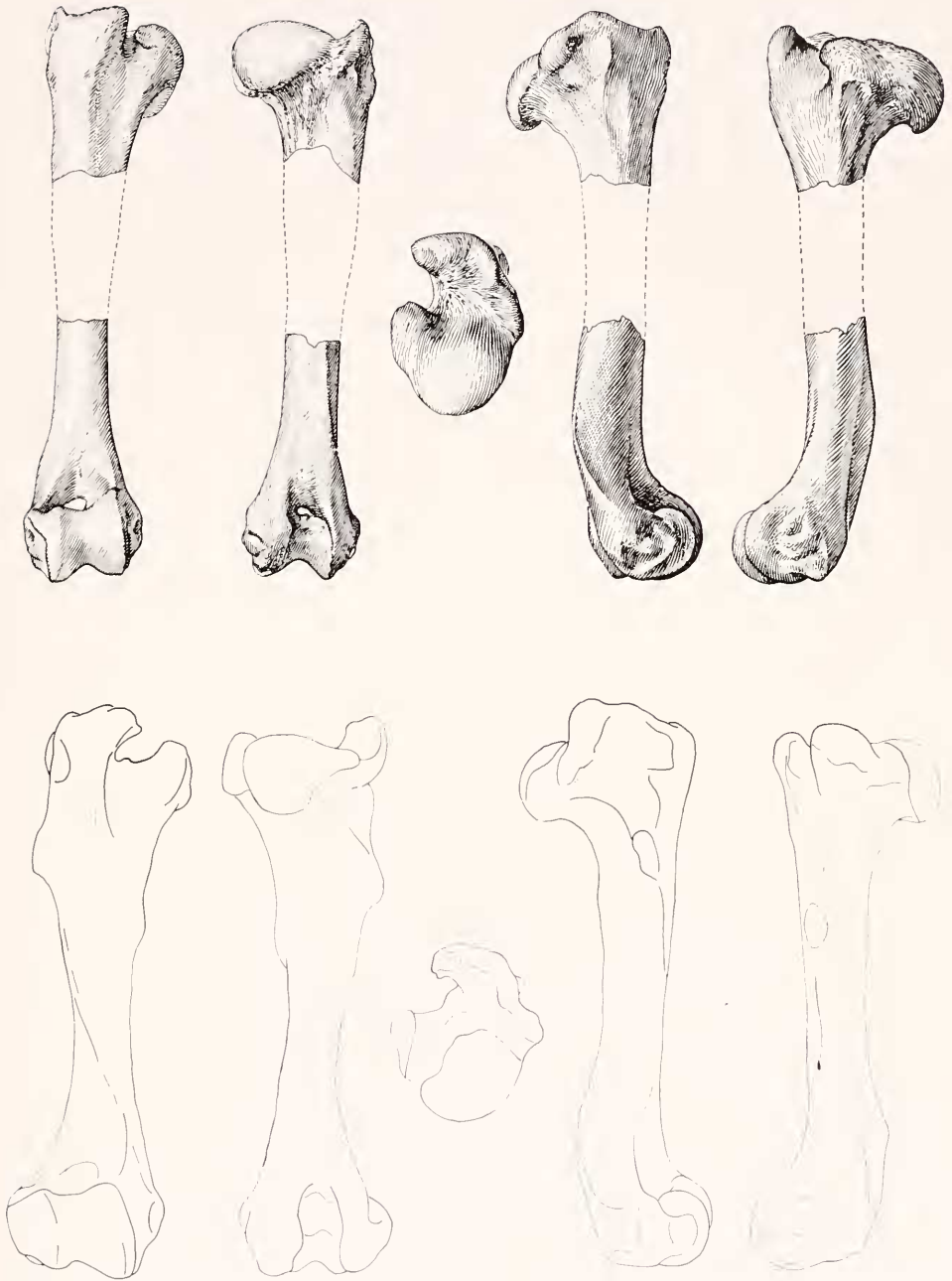
Fig. 7. Right humerus. Above, *Heptodon posticus*, MCZ 17670, in, from left to right, anterior, posterior, proximal, lateral and medial views. × ½. Below, *Tapirus pinchaque*, MCZ:M 6037, same views. × ¼.

of a deep coracoscapular (or supraspinous) notch.

Reduction of the acromion is an advanced feature in perissodactyls and appears to be correlated with loss of the clavicle. *Heptodon* may have still had a clavicle but if so, it probably was relatively small and did not articulate with the scapula. The absence of an acromion in *Tapirus* is reflected in modifications of the muscles which originally attached to that part of the scapula. These include the levator scapulae ventralis, which typically originates on the transverse processes of the atlas and inserts on the acromion, and the acromiodeltoid, which originates on the acromion and inserts on the deltoid tuberosity of the humerus. According to Campbell (1936, p. 206), in *Tapirus terrestris* the levator scapulae ventralis and acromiodeltoid have fused to form the transversohumeralis, which originates on the wing of the atlas and inserts on the fascia of the lateral head of the triceps.

A deep coracoscapular notch distinguishes scapulae of *Tapirus* from those of all other perissodactyls. The notch is formed by the dorsal expansion of the prominent tuber scapulae, possibly to extend the area available for attachment of the biceps. This expansion restricts the space open in front of the narrow neck of the scapula, thus forming the notch. The suprascapular artery and nerve pass through the coracoscapular notch. In life the notch is closed by a tendinous band which extends from the tip of the tuber scapulae to the anteroventral edge of the anterior border of the scapula.

Humerus (Fig. 7): The humerus of *Heptodon* is relatively long and slender. In MCZ 17670 it is 34 mm wide across the distal epicondyles and, judging from the proportions of the parts preserved, probably was about 150 mm long. The lateral (greater) tuberosity is raised slightly above the level of the head and extends anteriorly and then curves medially. The medial (lesser) tuberosity is short and low, and not distinctly

separated from the head. The bicipital groove is undivided and relatively deep and narrow. Much of the proximal half of the shaft is missing in MCZ 17670 and the proximal quarter is gone in AMNH 294 (*Heptodon calciculus*), but between the two specimens enough is preserved to indicate that the deltoid crest and tubercle were not prominent. The teres tubercle is not evident in AMNH 294; either the teres major left no attachment scar or it inserted relatively far proximally (on the missing proximal quarter of the shaft).

The supinator crest is relatively low but sharp-edged, and flares out posterolaterally along the distal third of the shaft. The coronoid (supratrochlear) fossa is relatively broad and shallow, and the olecranon (anconeal) fossa slightly narrower and deeper. The thin wall of bone separating the two is perforated but this may be artificial. The trochlea is asymmetrical, narrowing laterally. At the proximal end of the trochlea there is a thin strip of lateral condyle which rapidly narrows and terminates distally. Lateral and medial epicondyles are about equally prominent and both are relatively low.

The humerus of *Tapirus* differs from that of *Heptodon* in the following features: lateral tuberosity higher, with a more prominent, medially-directed anterior hook which is separated from the main ridge by a broad groove; medial tuberosity higher, raised above the level of the head and almost as high as the lateral tuberosity, separated from the head by a low groove, and with its medial face vertical; bicipital notch relatively wider; deltoid tubercle prominent, located almost one-third of the way down the shaft, with a narrow ridge continuing distally from it almost to the coronoid fossa; teres tubercle prominent, located one-third to one-half of the way down the shaft; supinator ridge not as extended proximally and blunter at its proximal end; distal end of shaft deeper anteroposteriorly; lateral condyle wider; coronoid fossa shallower, olec-
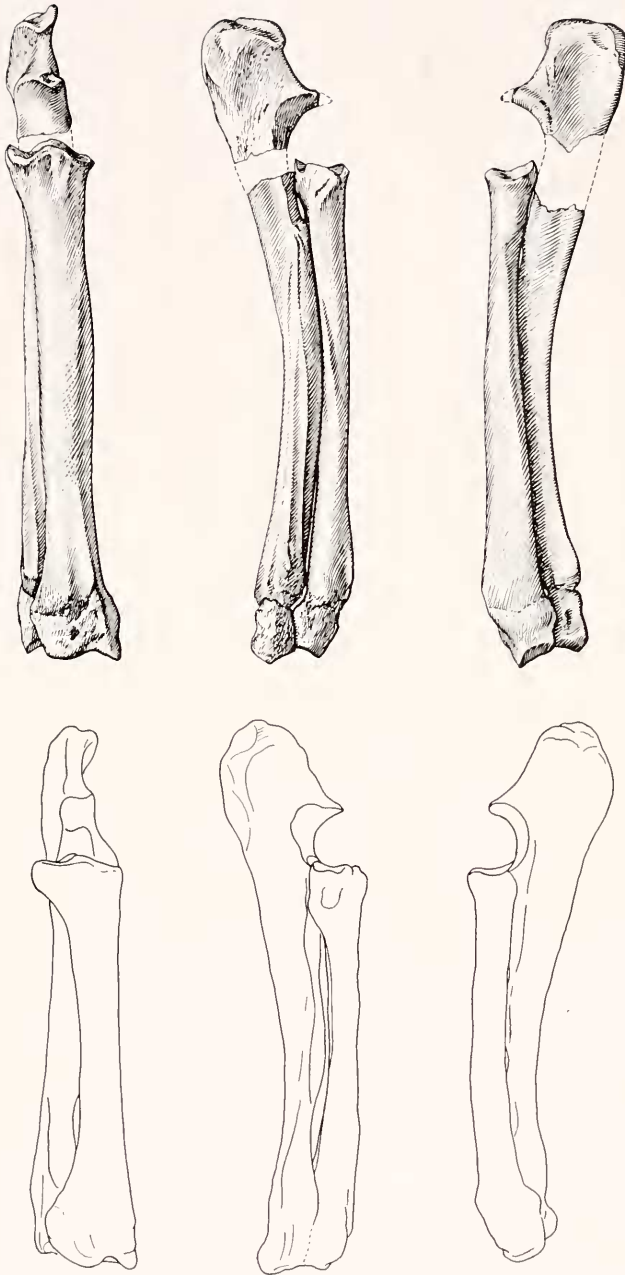
Fig. 8.   Right radius and ulna.   Above, *Heptodon pasticus*, MCZ 17670, in, from left to right, anterior, lateral, and medial views.   × ½.   Below, *Tapirus pinchaque*, MCZ:M 6037, in some views.   × ¼.

ranon fossa deeper, separated by very thin but unperforated sheet of bone; lateral epicondyle more massive and more posteriorly extended.

The more prominent tuberosities and tubercles for muscle attachment, the distal displacement of deltoid and teres tubercles, and the larger lateral epicondyle on the humerus of *Tapirus* correlate with the increased size and relatively heavier body of the modern tapir compared with that of *Heptodon*. Such modifications appear in all lines of perissodactyls with increase in size. The wider lateral condyle hinders lateral motion and thus stabilizes anterior–posterior movement at the elbow joint.

Radius (Fig. 8): The radius of *Heptodon posticus* in MCZ 17670 measures 139 mm long and 25 mm wide across the proximal end. The shaft is anteroposteriorly compressed and slightly arched anteriorly. The humeral facet is relatively short (anteroposteriorly) and wide, and divided into two shallow concavities, the lateral one shorter and wider than the medial one. A slightly roughened area on the anterior face of the shaft a short distance below the humeral facet marks the lateral end of the insertion of the biceps; the biceps aponeurosis probably extended around onto the medial side of the radius. A vertical scar on the anteromedial edge and medial side of the shaft, beginning about 20 mm below the proximal end, indicates the insertion of the brachialis and possibly also a medial collateral ligament. Just below the humeral facet on the lateral side of the shaft a small tuberosity marks one part of the origin of the lateral digital extensor (extensor digiti quinti proprius), and probably the insertion of lateral collateral ligaments. A line which begins about one-quarter of the way down the lateral side of the shaft and curves anteriorly as it descends, marks the anterior edge of the radial origin of the extensor carpi obliquus (abductor pollicis longus).

On the posterior side of the shaft, just below the humeral facet, there is a narrow facet for articulation with the ulna. Below this facet there begins a roughened and slightly excavated area marking the attachment of the interosseus ligaments which bound the radius to the ulna. Proximally, this scar extends across the entire width of the shaft, but about halfway down it is confined to the lateral side of the shaft. About 15 mm below the proximal end of the shaft the scar is interrupted by the interosseus space, a smooth area marked by the passage of the interosseus artery.

The distal end of the shaft of the radius is somewhat expanded and bears on its anterior face a broad groove for the passage of the tendon of the extensor carpi radialis. A small facet for articulation with the distal end of the ulna is present on the posterolateral corner. The distal end of the radius bears a large, anterolaterally concave, posteriorly convex facet for the scaphoid and an anteriorly concave, posteriorly convex facet for the lunar.

Ulna (Fig. 8): The ulna has a mediolaterally compressed, anteriorly arched shaft, and a moderately large olecranon process. The anterior edge of the shaft is roughened along its entire length, except for small proximal and distal facets for the radius and a small interosseus space, indicating that the ulna was firmly and probably immovably bound by interosseus ligaments to the radius. The olecranon is slightly concave medially and expanded on proximal and posterior sides. A large rounded prominence occupying the posterior half of the end of the olecranon marks the main area of insertion of the long head of the triceps; the lateral and medial heads of the triceps inserted on lateral and medial sides, respectively, below the insertion of the long head.

The lateral side of the shaft of the ulna bears a long vertical scar from the origin of part of the lateral digital extensor and, between this and the radius, is roughened from the attachment of the oblique carpal
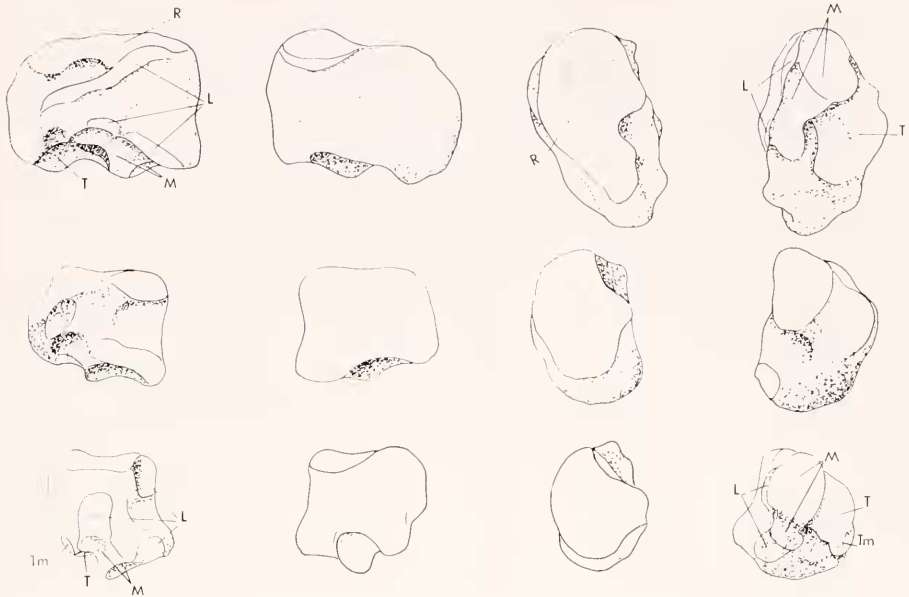
Fig. 9. Right scaphoid. Top row: *Heptodon posticus*, MCZ 17670, in, from left to right, lateral, medial, proximal and distal views. × 1½. Middle row: *Pratapirus abliquidens*, AMNH 662 (reversed), × ¾. Bottom row: *Tapirus pinchaque*, YPM 204, × ½. Letters indicate articular contacts. For abbreviations see p. 102.

extensor. The anterior edge of the medial side of the ulna bears scars just below the coronoid crest, marking the insertions of the biceps and brachialis. Distally, the shaft of the ulna is excavated to fit the swollen distal end of the radius, and there is a small anteromedial facet for articulation with the radius. The distal end of the ulna bears a roughly square, saddle-shaped facet for articulation with the cuneiform and, posterior to it, a slightly smaller, triangular, convex, posteromedially-facing facet for the pisiform.

The radius and ulna of *Tapirus* differ from those of *Heptodon* in the following features: radius and ulna fused together proximally and distally; humeral facet of radius further extended laterally, and lateral tuberosity more prominent; distal end of radius wider, with most of the expansion on the lateral side; facet for lunar (at distal end of radius) shorter anteroposteriorly.

Carpus: The carpus, seen in anterior view, is relatively low and wide, with the lunar resting mainly on the unciform. The scaphoid (see Fig. 9) is relatively long (anteroposteriorly) and low, with a large posterior process. The proximal surface is covered by an anteromedially convex, posterolaterally concave facet for the radius, and the lateral side bears narrow proximal and distal strips for articulation with the lunar. On the distal surface there are two lateral facets, the posterior one steeply inclined and the anterior one horizontal, for the magnum, and a large medial facet for the trapezoid. There is no evidence of a facet for the trapezium.

The lunar (see Fig. 10) is relatively high and narrow in anterior view. The facet for the radius is wide and anteroposteriorly convex anteriorly, and narrow and relatively flat posteriorly. The medial side has narrow proximal and central facets for the scaphoid and, anteriorly, a large, vertical, distal facet for the magnum. Posteriorly, the mediodistal edge is truncated by a large concave facet for the hump of the magnum.
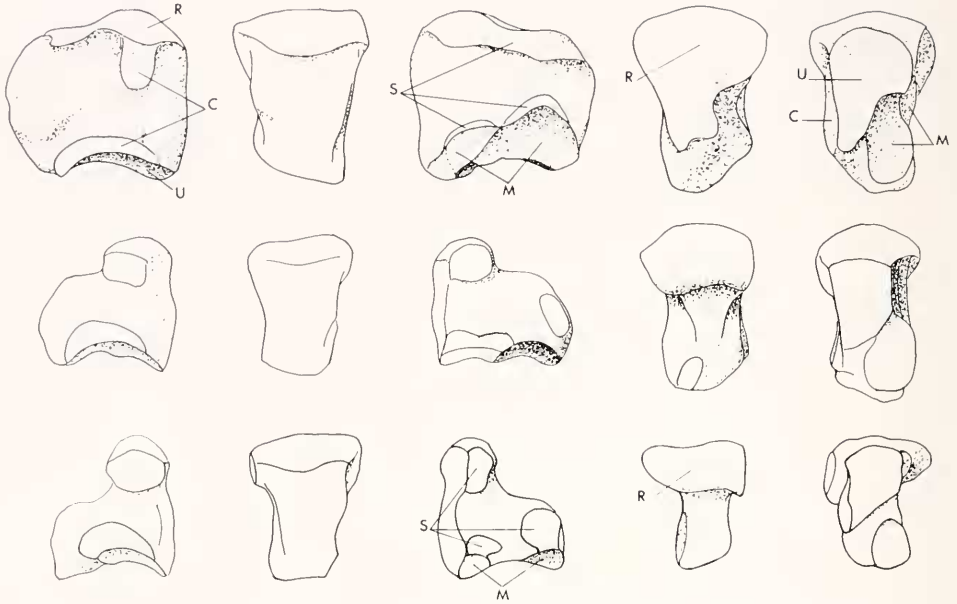
Fig. 10. Right lunor. Top row: *Heptodon posticus*, MCZ 17670, in, from left to right, lateral, anterior, medial, proximal, and distal views. × 1½. Middle Row: *Protapirus obliquidens*, AMNH 662 (reversed), × ¾. Bottom row: *Tapirus pinchaque*, YPM 204, × ½. Letters indicote orticular contacts.

Anteriorly, the distal surface is covered by an anteroposteriorly concave, horizontal facet for the unciform. The lateral side has relatively small proximal and distal facets for the cuneiform.

The cuneiform (see Fig. 11) has a roughly square, anteroposteriorly concave, slightly lateromedially convex ulnar facet, and a slightly smaller, elongate, posteriorly inclined pisiform facet. The medial side has relatively short proximal and distal facets for the lunar, and the distal surface bears a large, triangular, concave facet for the unciform.

The pisiform (see Fig. 11) has approximately equal-sized facets for ulna and cuneiform, and a relatively flat, slightly proximodistally expanded posterior process. A prominent tubercle on the anterior end of the medial side may have served for the attachment of ligaments which bound the pisiform to the rest of the carpus.

The trapezium (see Fig. 12) is a small, relatively flat, disc-shaped bone, with a large lateral facet for articulation with the trapezoid. The trapezoid is relatively long anteroposteriorly and low, with a large, saddle-shaped facet for the scaphoid occupying the proximal surface, and a facet for the second metacarpal covering most of the distal surface. Facets for the magnum and trapezium occur on lateral and posteromedial sides, respectively.

The magnum (see Fig. 12) has an approximately square anterior face, a short, high dorsal hump, and a large posterior process. Articulation with the scaphoid is in two parts, a horizontal anterior facet and an almost vertical posterior one (on the medial side of the dorsal hump). Articular facets for the lunar, on the other hand, are vertical in front and more horizontal (laterodistally inclined) behind, with the posterior one covering the top of the dorsal hump. On the medial side there are facets for the trapezoid and second metacarpal, and on the lateral side, below the anterior lunar facet, a small facet for the unciform.
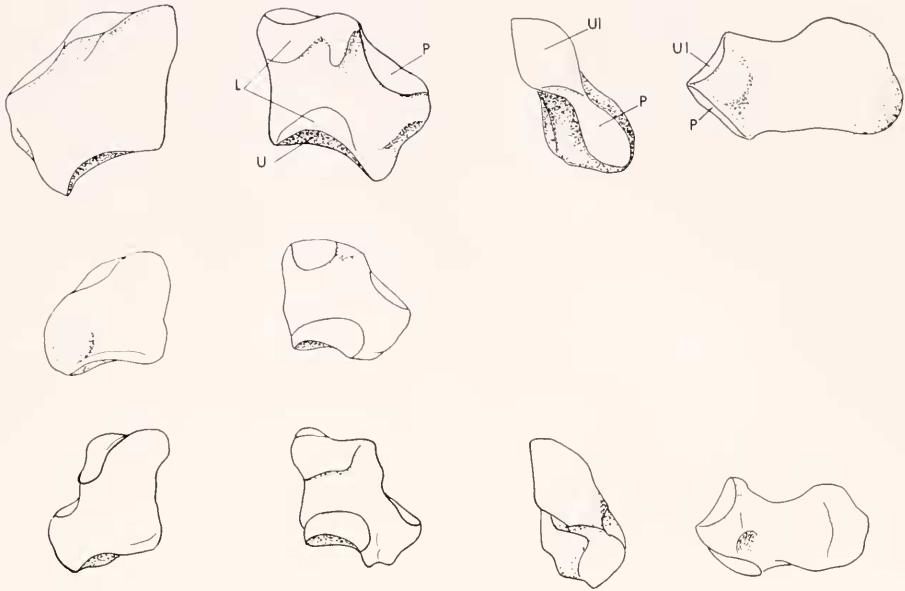
Fig. 11. Right cuneiform and pisiform. Top row: *Heptodon pasticus*, MCZ 17670, cuneiform in lateral, medial and proximal views, and pisiform in medial view. × 1½. Middle row: *Protapirus obliquidens*, AMNH 662 (reversed) × ¾. Bottom row: *Tapirus pinchaque*, YPM 204, × ½. Letters indicate articular contacts.

A saddle-shaped facet for the third metacarpal occupies the anterior half of the distal surface.

The unciform (see Fig. 12) is about as high as it is wide, and has a relatively short, stubby posterior process. The proximal surface bears approximately equal-sized, slightly convex lunar and cuneiform facets. Along the curving mediodistal edge there is a small proximal facet for the magnum, a central facet for the proximolateral edge of the third metacarpal, and a large, posteriorly-expanded distal facet for the fourth metacarpal. The same articular strip continues proximolaterally for articulation with the fifth metacarpal.

Metacarpals: There is no evidence of a first metacarpal. The second metacarpal is 72 mm long and 11 mm wide at the distal end. It has a relatively long, saddle-shaped facet for the trapezoid, a narrow lateral articular strip for the magnum, and a postero-medial facet for the trapezium. A broad, low tuberosity on the posterior side, im-

mediately below the trapezoidal facet, may have served for attachment of the flexor carpi radialis, or possibly a carpal ligament.

The third metacarpal is 83 mm long and 14 mm wide across the distal condyle. At the proximal end there is a large, antero-posteriorly convex, mediolaterally concave, facet for the magnum, and a smaller antero-laterally-facing facet for the unciform. A low prominence on the medial side of the anterior face, just below the magnum facet, marks the insertion of the extensor carpi radialis. The shaft of the third metacarpal is triangular in cross section proximally and flat distally, with posterolateral and postero-medial sides roughened proximally for the attachment of the interossei. The distal condyle is evenly convex and has a prominent medial keel on the posterior half. Two pits on the posterior face, immediately above the condyle, accommodated the proximal ends of the sesamoids. On each side of the condyle a deep pit surmounted by a low tuberosity marks the attachment of deep
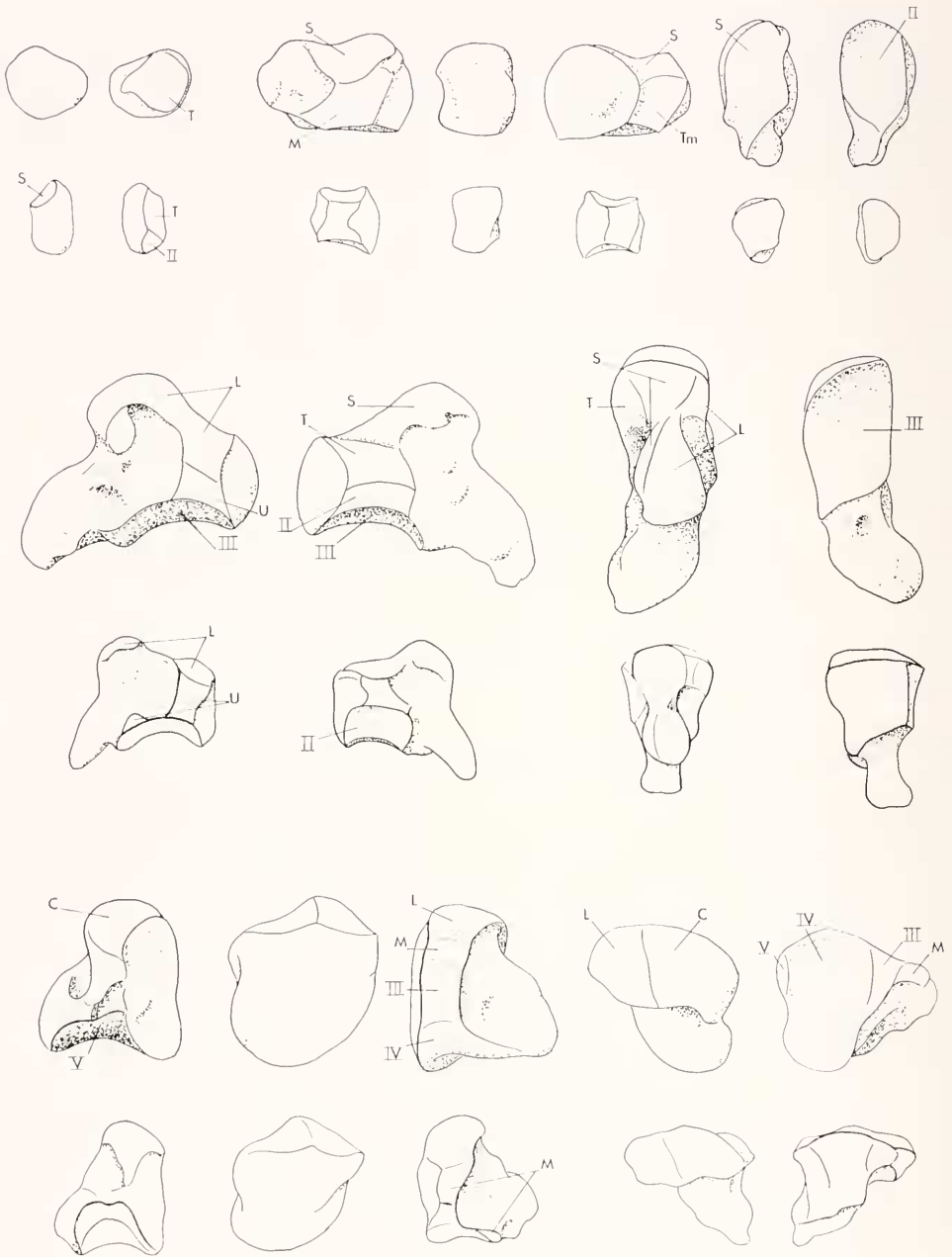
Fig. 12.   Right distal carpals.   In each pair of rows *Heptodon posticus*, MCZ 17670, is above, × 1½, and *Tapirus pinch-aque*, YPM 204, is below, × ½.   Top two rows: From left to right, trapezium in medial and lateral views, and trape-zoid in lateral, anterior, medial, proximal and distal views.   Middle two rows: magnum in lateral, medial, proximal and distal views.   Bottom two rows: unciform in lateral, anterior, medial, proximal and distal views.   Letters indi-cate articular contacts.

and superficial layers, respectively, of collateral ligaments. The distal ends of the second, fourth, and fifth metacarpals are similar to that of the third, but are transversely compressed and asymmetrical.

The fourth metacarpal has approximately the same dimensions as the second. It has a large triangular proximal facet for the unciform and a small lateral facet for the fifth metacarpal. The fifth metacarpal is 58 mm long and 9 mm wide distally, with an elongate, saddle-shaped unciform facet and a narrow medial facet for the fourth metacarpal.

Phalanges: The proximal phalanx of the medial digit is about 21 mm long. Prominent raised areas on the posterior face just below the metacarpal facet served for attachment of the collateral ligaments; the sesamoidean ligaments probably inserted on the area between them. Tuberosities on left and right sides at the distal end of the posterior face probably mark insertions of parts of the tendo perforatus (superficial digital flexor tendon). On either side of the distal articular facet, a shallow pit surmounted by a low tuberosity indicates the attachment area of the collateral ligament and suspensory ligament of the navicular sesamoid.

The second phalanx of the third digit is about 13 mm long and 13 mm wide across its proximal end. Low prominences at the proximal end of the posterior face served for insertion of part of the tendo perforatus, and, laterally, the collateral ligaments. Shallow depressions on each side of the distal condyle indicate attachment areas of collateral ligaments to the third phalanx.

The third, or ungual, phalanx of the median digit measures about 20 mm long and has a maximum width of 16 mm. The medial fissure is very short. A large raised area on the proximal end of the posterior surface marks the insertion of the tendo perforans (deep digital flexor tendon). On either side of this raised area, shallow depressions indicate the insertion areas of the collateral
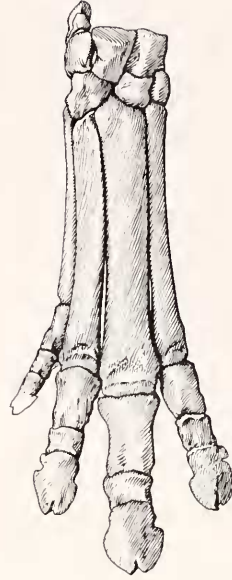

Fig. 13. Right manus of *Heptodon posticus*. MCZ 17670. × ½.

ligaments. Two large foramina above the tendo perforans prominence served for the entrance of the digital arteries into the ungual. Phalanges of the other digits are similar to those of the third, but are asymmetrical and more transversely compressed.

The complete manus of *Heptodon posticus* is shown in Figure 13.

The manus of *Tapirus* differs from that of *Heptodon* in the following features: Scaphoid shortened by truncation of the posterior tuberosity and posterior end of the radial facet; trapezium-scaphoid articulation present; scaphoid-lunar articular facets relatively higher (proximodistally), the proximal one confined to the anterior end and oriented posterolaterally so that the scaphoid curves behind the anterior edge of the lunar. Lunar with posterior part of proximal surface excavated so that the radial facet is confined to the anterior third of the bone and the proximal half of the posterior tuberosity is missing; distal lunar-cuneiform and lunar-unciform articulations shorter posteriorly; lunar-magnum facets

more horizontally oriented; posterior lunar-magnum facet relatively smaller. Cuneiform with posterior part of proximal surface lower, resulting in a more distally located pisiform facet. Trapezium relatively higher. Trapezoid relatively shorter (anteroposteriorly) and higher, with less of a posterior process. Magnum with a relatively lower and wider anterior face and a shorter and less pointed posterior process; magnum-unciform articulation relatively higher, but lacking a separate posterior facet; magnum-second metacarpal facet higher proximodistally. Metacarpals relatively shorter and wider.

The main difference between the front foot of *Tapirus* and that of *Heptodon* is in the radio-carpal joint. The truncation of the posterior end of the scaphoid and lowering of the posterior half of the lunar produces a posteriorly-shortened articulation between the radius and the scaphoid and lunar. This difference, plus the lower pisiform facet on the cuneiform, suggests greater freedom for flexion at this joint in *Tapirus*. The lateral extension of the proximal surface of the scaphoid behind the proximal facet of the lunar strengthens the scapho-lunar articulation and also provides additional support for the radius (possibly to compensate for the shortened radio-lunar articulation). Most of the other differences listed above are either related to the modification just discussed or, like the more horizontal lunar-magnum facets, result from the greater weight of *Tapirus*.

The manus of *Protapirus* was described and figured most recently by Scott (1941, pp. 756–758, pl. 80, fig. 2), based on a late Oligocene specimen (AMNH 662). It is generally quite similar to the manus of *Tapirus*, but slightly more primitive in the following features: scaphoid and trapezoid relatively longer anteroposteriorly; posterior process of lunar and cuneiform relatively
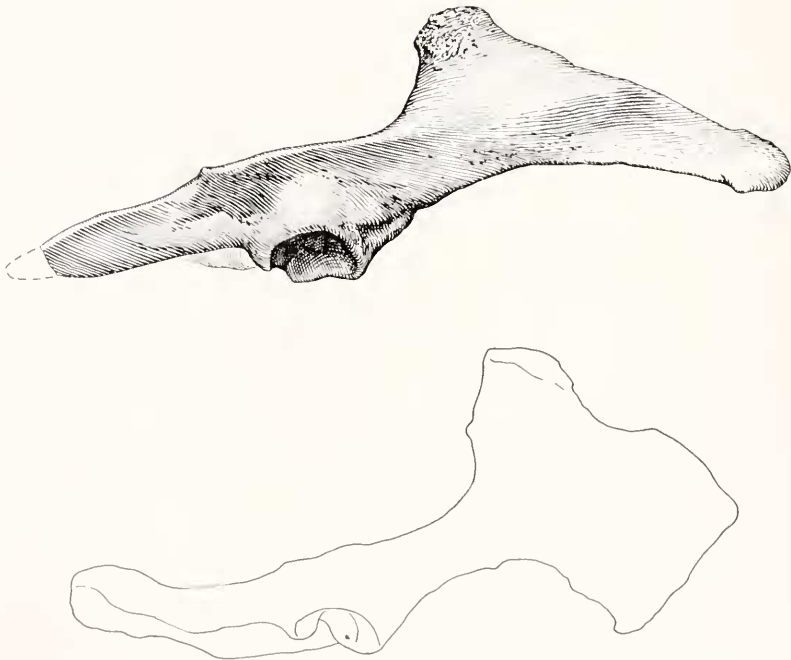

Fig. 14. Right innominate. Above, *Heptodon pasticus*, MCZ 17670, lateral view, × ½. Below, *Tapirus pinchaque*, MCZ:M 6037. × ¼.

higher; distal lunar-cuneiform articulation extends further posteriorly; trapezium extends posterolaterally instead of posterodistally. The manus of *Protapirus* further differs from that of *Tapirus* in having a relatively larger trapezium, a more posteriorly and more proximally located scaphoid-lunar articulation, and relatively shorter phalanges. On the scaphoid the posterior lunar facet is separated from the trapezoid facet by a large fossa. The carpus of *Protapirus* is not relatively longer and narrower than that of *Tapirus*, contrary to the statements of Scott (*op. cit.*, p. 758).

A second manus of *Protapirus* (Univ. Calif. Mus. Paleo. 934), representing *P. robustus*, a larger species than the one Scott described, differs in no appreciable way from AMNH 662 except in larger size.

The lunar, cuneiform, and pisiform are all that is known of the carpus of the early Miocene genus *Miotapirus*. The posterior processes of the lunar and cuneiform are as low in *Miotapirus* as in *Tapirus*, but the distal lunar-cuneiform articulation is still longer and the posterior scaphoid facet of the lunar more posteriorly and proximally located than in the modern tapir.

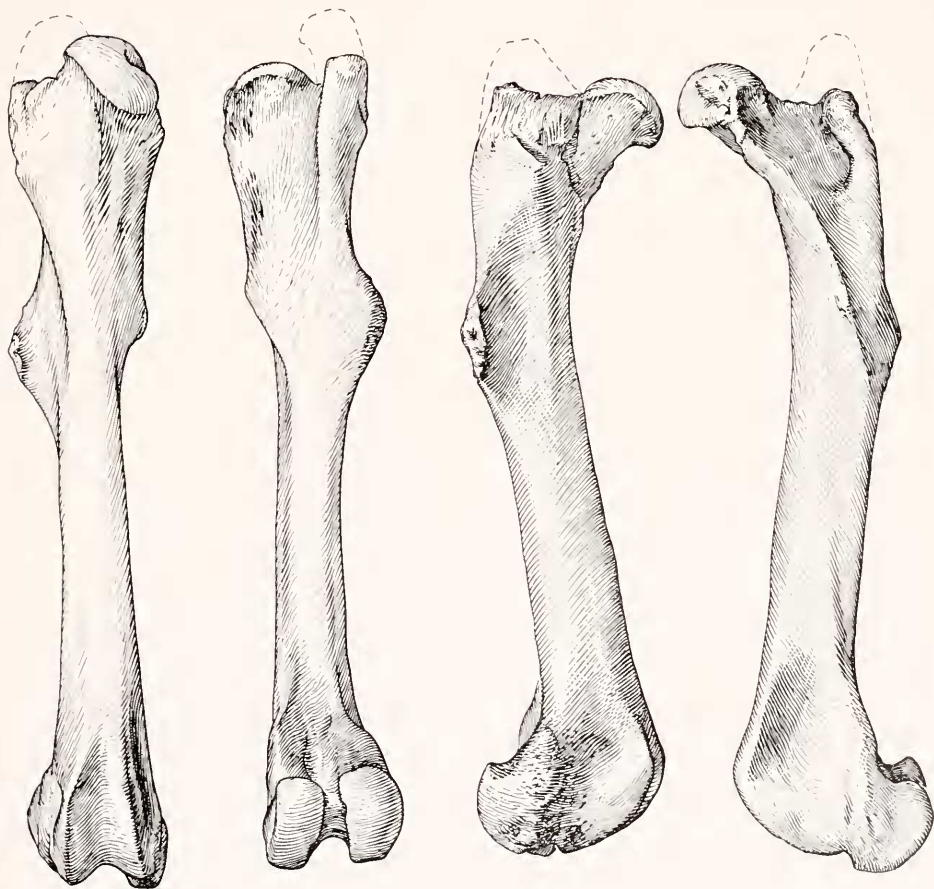*Innominate* (Fig. 14): The blade of the ilium is expanded dorsally into a relatively

Fig. 15. *Heptodon posticus.* MCZ 17670. Right femur in, from left to right, anterior, posterior, lateral and medial views. × ½.
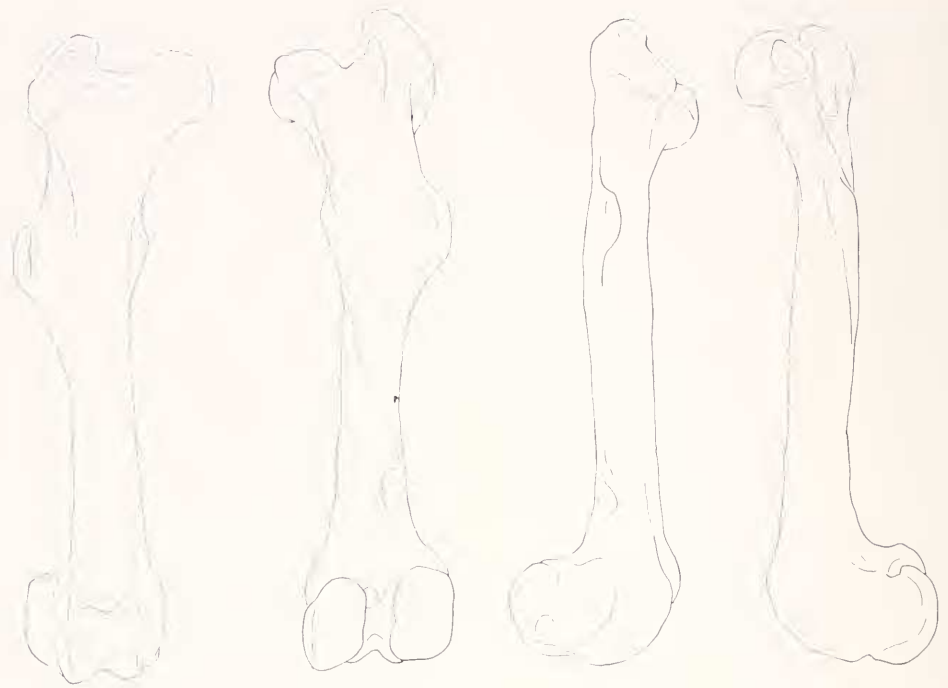
Fig. 16.   *Tapirus pinchaque.*   MCZ:M 6037.   Right femur in, from left to right, anterior, posterior, lateral and medial views. $\times$ ¼.   Compare with Fig. 15.

narrow tuber sacrale, and extends relatively far anterolaterally to terminate in a narrow tuber coxae. Between these two tuberosities, the iliac crest is straight. The shaft of the ilium is relatively long and narrow. On the lateral side, just in front of the acetabulum, a prominent groove and ridge mark the origin of the lateral tendon of the rectus femoris. The ischiatic spine is located on the dorsal border a short distance posterior to the acetabulum. The posterior end of the ischium is broken off, but judging from its condition in *Hyrachyus* and *Helaletes*, it probably was considerably shorter than the ilium, and the tuber ischii was probably relatively weak. Pelvic girdles in which the ilium is relatively long and pubo-ischiac portion relatively short are characteristic of cursorial ungulates, and indicate an increase in importance of the gluteal muscles (which originate on the blade of the ilium) over those of the pubo-ischiac group in extension

of the femur (Smith and Savage, 1956, pp. 612–614).

The innominate of *Tapirus* differs from that of *Heptodon* in having a much wider, more vertically expanded, tuber coxae, and relatively larger sacral and ischial tuberosities. The tuber coxae serves for attachment of the external and internal obliquus abdominis muscles, the tuber sacrale for sacral ligaments medially and parts of the gluteus medius and longissimus dorsi on its lateral surface, while the tuber ischii serves for the origin of biceps femoris, semimembranosus, and semitendinosus. The greater prominence of these tuberosities in the modern tapir probably correlates with its larger size and relatively heavier body.

Femur (Fig. 15):   The femur of *Heptodon posticus* measures about 205 mm long from head to distal condyles) and 37 mm wide across the distal end. The top of the greater trochanter has been broken off in
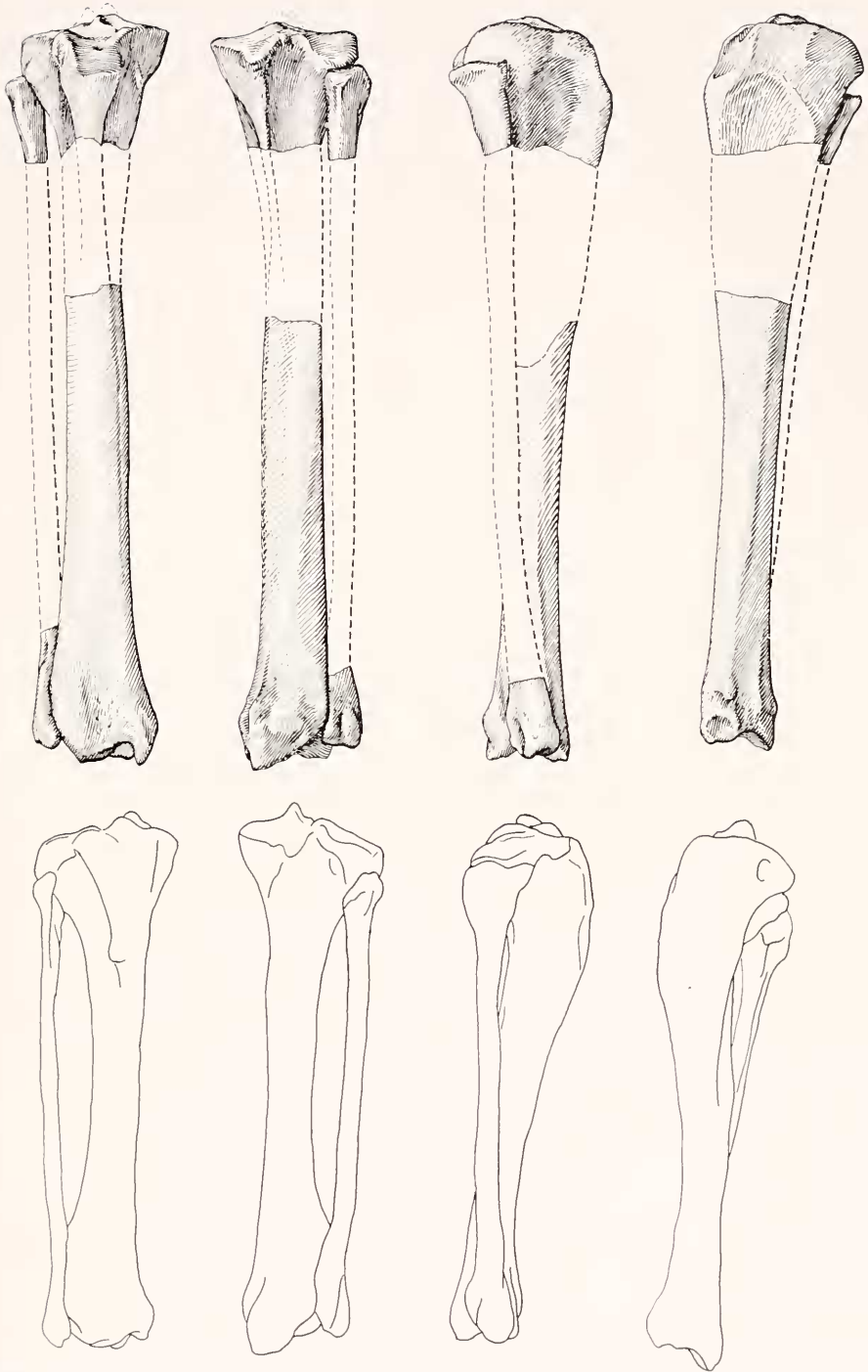
Fig. 17. Right tibia and fibula. Above, *Heptodon posticus*, MCZ 17670, in, from left to right, anterior, posterior, lateral and medial views. ✕ ½. Below, *Tapirus pinchaque*, MCZ:M 6037, in same views. ✕ ¼.

MCZ 17670, but judging from its condition in *Heptodon calciculus* and *Hyrachyus*, it must have extended above the level of the head. The head is hemispherical and extends anteromedially on a relatively long and thin neck. (There may have been a small amount of post-mortem anterior displacement of the head in MCZ 17670.) The trochanteric ridge is fairly prominent, and extends distally almost to the level of the lesser trochanter. The lesser trochanter is located slightly less than one-third of the way down the shaft, and the large third trochanter is situated slightly lower on the opposite side. A supracondyloid fossa, marking the origin of the plantaris, is evident on the posterior side of the shaft above the condyles. At the distal end of the femur, the trochlea is relatively narrow and almost symmetrical. Medial and lateral epicondyles are low. Pits for the popliteus and extensor digitalis longus are present on the lateral epicondyle. Lateral and medial condyles are separated by a deep intercondyloid fossa.

The femur of *Tapirus* (see Fig. 16) differs from that of *Heptodon* mainly in being slightly more robust, with wider trochlea and condyles and more massive epicondyles (especially the lateral one). The lesser and third trochanters in *Tapirus* are located about one-third of the way down the shaft. These differences are probably accounted for mainly by the larger size of the modern tapir.

Tibia (Fig. 17): The tibia of *Heptodon posticus* preserved in MCZ 17670 is missing about one-quarter of the shaft and it is not possible to determine its length. In *H. calciculus* (AMNH 294) the tibia is about as long as the femur. The proximal end of the tibia is about as deep anteroposteriorly as it is wide. The spine, or intercondyloid eminence, is broken off. The cnemial crest is fairly prominent and bears a large depression proximally for the middle patellar ligament. At the distal end of the shaft the medial malleolus is prominent and bears a large smooth scar from attachment of the

medial ligament. Posterior to the medial malleolus is a groove for the tendon of the flexor digitalis longus. On the lateral side there is a facet for articulation with the distal end of the fibula. The articular grooves for the astragalus are relatively deep, with the medial one narrower than the lateral one.

The tibia of *Tapirus* differs from that of *Heptodon* mainly in being relatively slightly more robust, with relatively wider proximal and distal articular surfaces and a more laterally expanded tuberosity (at the head of the cnemial crest). These differences may be accounted for by the larger size of the modern tapir. The laterally expanded tuberosity provides a greater area for attachment of the lateral patellar ligament and the fascia lata. In *Tapirus* the medial intercondyloid tubercle is higher than the lateral one, the reverse of the condition in *Heptodon*. The same change in relative heights of these tubercles occurred in equoid evolution (Kitts, 1956, p. 26). Increase in height of the medial tubercle would help prevent lateral dislocation of the femur relative to the tibia and might be correlated

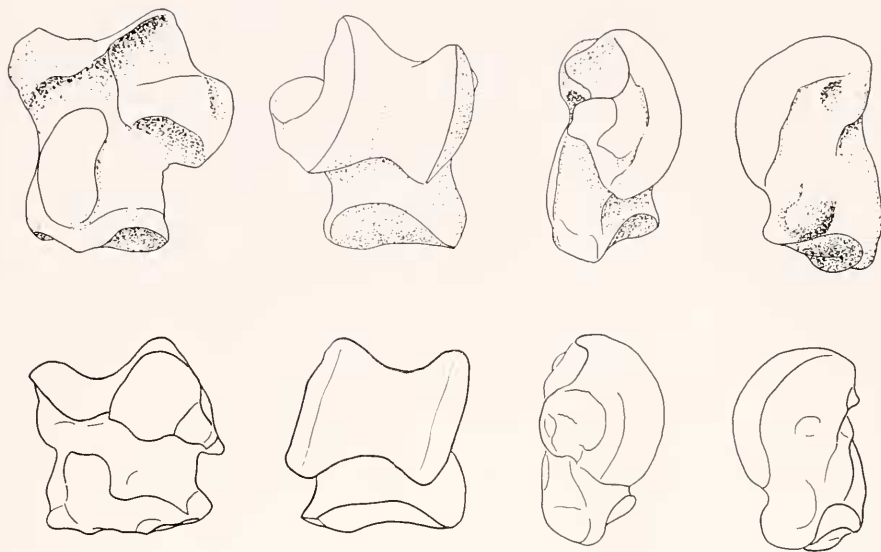Fig. 18. *Heptodon posticus.* MCZ 17670. Right tarsus and proximal portions of metatarsals. × ½.

Fig. 19. Right astragalus. Above, *Heptodon posticus*, MCZ 17670, in, from left to right, posterior, anterior, lateral and medial views. Natural size. Below, *Tapirus pinchaque*, YPM 204, in same views. × ½.

with the relative increase in size of the lateral epicondyles (indicating more powerful extensor musculature) on femora of large perissodactyls.

Fibula (Fig. 17): Proximal and distal ends of the fibula are present in MCZ 17670 and indicate a relatively thin but complete bone which articulated with, but was not fused to, the tibia. The proximal articular surface is elliptical in outline and horizontally oriented. The distal end is expanded and has a vertical groove in its posterolateral side for the tendon of the peroneus brevis (lateral digital extensor). Distally, the medial surface forms the lateral side of the lateral articular groove for the astragalus.

The fibula of *Tapirus* is similar to that of *Heptodon*, differing only in having an oblique facet for the proximal articulation with the tibia. The lateral condyle of the tibia entirely covers the head of the fibula in *Tapirus*, while in *Heptodon* it is partly exposed.

Tarsus (Fig. 18): Seen in anterior view the tarsus of *Heptodon* is relatively high and narrow. The astragalus rests on the cuboid posteriorly but anteriorly the two are separated by a small calcaneum-navicular articulation. The ectocuneiform extends further distally than the cuboid or mesocuneiform so that it articulates with second and fourth metatarsals as well as the third.

In *Heptodon posticus* the trochlea of the astragalus (see Fig. 19) is about as high as it is wide, and has a relatively broad, shallow median groove. In *H. calciculus* the trochlea is relatively higher and narrower. The neck is relatively long and diverges slightly from the line of the trochlear crests. On the posterior (plantar) side of the astragalus the two main faces of the proximal calcaneal articulation are approximately perpendicular to each other. The sustentacular facet is relatively long and slightly proximodistally convex. The distal calcaneal facet is a long, low strip which in MCZ 17670 (*H. posticus*) does not, but in AMNH 294 (*H. calciculus*) does, contact the sustentacular facet. On the distal end of the astragalus the navicular facet is slightly wider than long, and is convex anteroposteriorly and slightly concave mediolaterally.
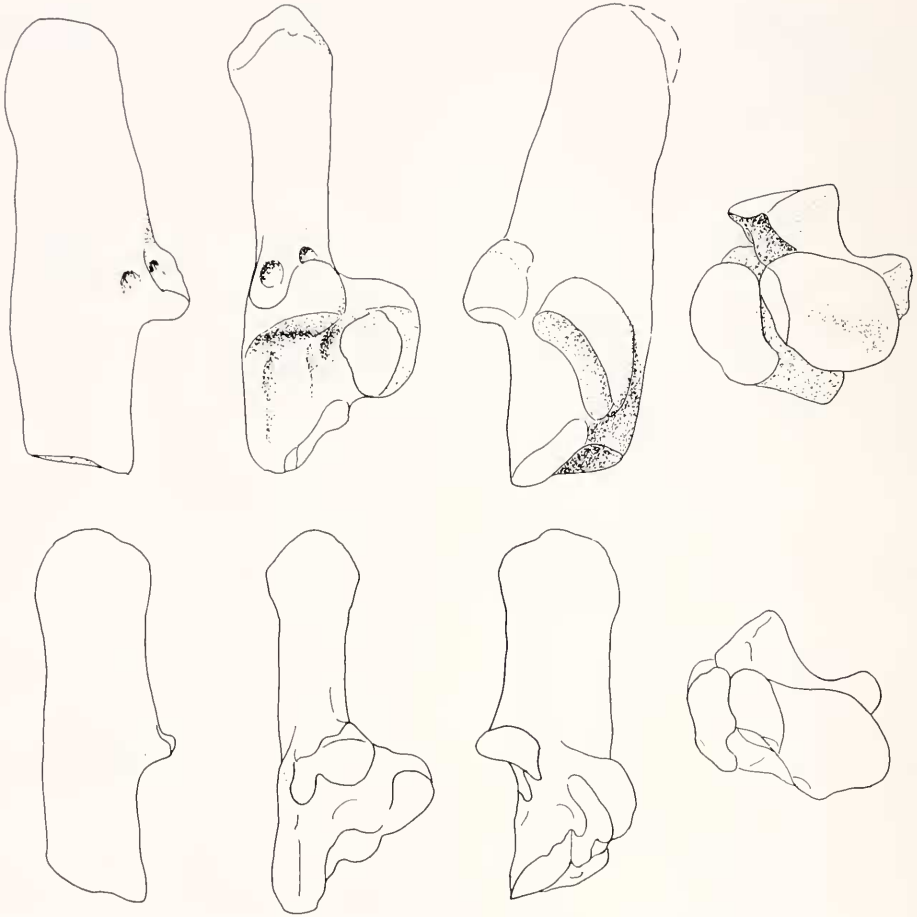
Fig. 20. Right calcaneum and astragalus. Above, *Heptodon posticus*, MCZ 17670, in, from left to right, lateral, anterior and medial views of calcaneum and distal view of astragalus and calcaneum. Natural size. Below, *Tapirus pinchaque*, YPM 204, in same views. × ½.

The cuboid facet is a relatively narrow, laterodistally-facing strip and does not reach the anterior edge of the astragalus. On the lateral side of the trochlea a broad pit marks the insertion of the short lateral ligament. On the medial side a shallow proximal pit indicates the insertion of the short medial ligament, while a tuberosity at the distal end of the neck marks the attachment area of the dorsal ligament.

The calcaneum (see Fig. 20) is relatively long and thin, with the lateral astragalar facet located slightly closer to the distal

than proximal end. The tuber calcis is mediolaterally compressed and slightly expanded at its free end. The two major planes of the lateral astragalar facet meet at a right angle. A prominent pit just above this facet accommodated the distal end of the fibula in extreme flexion of the tibio-tarsal joint. The sustentaculum is slightly higher than wide and bears an irregularly oval, slightly concave facet for the astragalus. A long, low facet on the distal end of the medial side of the body articulates with the navicular anteriorly and with the astrag-
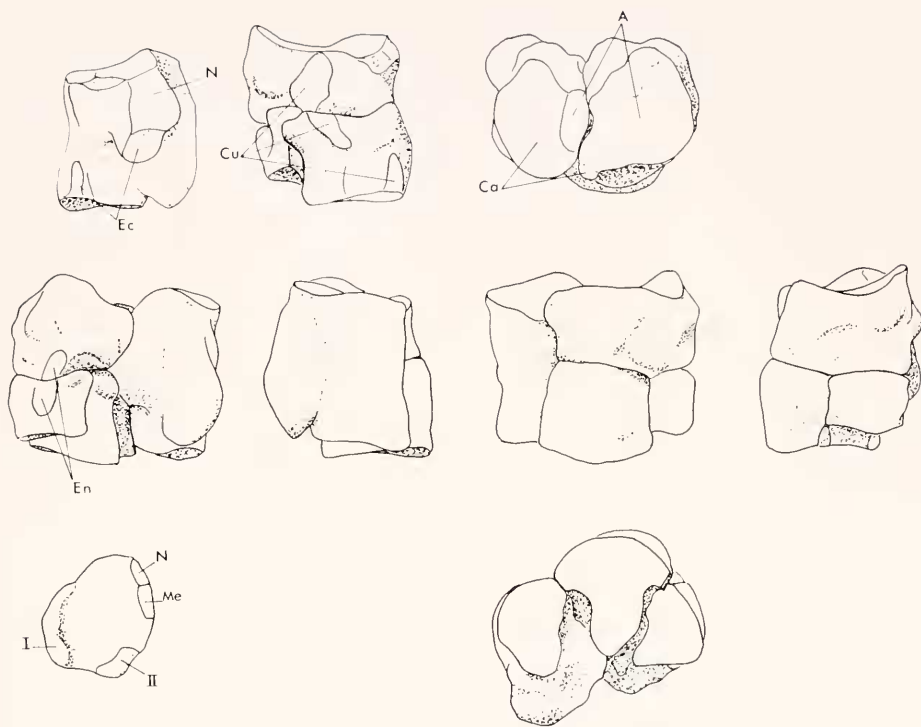
Fig. 21. *Heptodon posticus.* MCZ 17670. Right distal tarsals. Top row: (from left to right) cuboid, medial view; navicular, ecto- and mesocuneiforms, lateral view; cuboid and navicular, proximal view. Middle row: distal tarsals in, from left to right, posterior, lateral, anterior and medial views. Bottom row: entocuneiform in anterolateral view and cuboid, ecto- and mesocuneiforms in distal view. All natural size. Letters indicate articular contacts.

alus for most of its length. An irregularly oval, saddle-shaped cuboid facet occupies the entire distal end of the calcaneum. A pit on the lateral side of the calcaneum at the level of the lateral astragalar facet presumably marks the insertion of part of the short lateral ligament.

The cuboid (see Fig. 21) is relatively high and narrow, with a moderately large posterior tuberosity. The saddle-shaped calcaneal facet shares the proximal surface with a small elongate astragalar facet which does not reach the front of the cuboid. The proximal half of the medial side of the cuboid bears a small anterior facet and a large slightly concave posterior facet for the navicular. Just below the latter is a medio-distally inclined facet for the ectocuneiform. There is also a small anterior facet for the

ectocuneiform. The facet for the fourth metatarsal covers the distal surface.

The navicular is about as wide as it is deep (anteroposteriorly) with a saddle-shaped proximal surface for articulation with the astragalus. A small oblique facet at the anterolateral corner articulated with the calcaneum. The lateral side bears a large, gently convex posterior facet and a small anterior facet for the cuboid. On the posterior side there is a posterodorsally-facing facet for the entocuneiform. The distal surface bears a large triangular facet for the ectocuneiform and a small, roughly quadrangular facet for the mesocuneiform.

The ectocuneiform is triangular in proximal view and slightly higher than the navicular. In the articulated tarsus it extends further distally than the cuboid or meso-
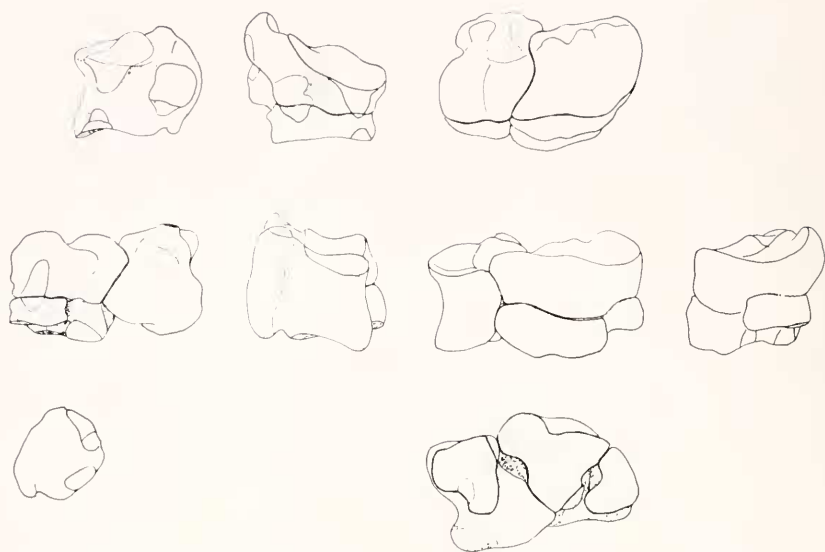
Fig. 22. *Tapirus pinchaque*. YPM 204. Right distal tarsals. Compare with Fig. 21. × ½.

cuneiform and has small distal facets on medial and lateral sides for the second and fourth metatarsals, respectively. It has a vertical anterior facet and a proximolaterally-facing posterior facet on the lateral side for articulation with the cuboid, and a large proximal facet for the mesocuneiform on the medial side. Distally, the ectocuneiform articulates with the third metatarsal by a relatively flat facet.

The mesocuneiform is small and roughly triangular in horizontal section. On its lateral side it has a proximal facet for the ectocuneiform and on its medial side a large proximal facet for the entocuneiform.

The entocuneiform and vestigial first metatarsal were briefly described in a previous paper (Radinsky, 1963b). The entocuneiform is roughly circular in posterior view, and relatively flat and anteroposteriorly compressed. On its anteromedial edge it bears adjacent facets for the navicular and mesocuneiform, and a short distance distally from these, a long facet for the second metatarsal. On the anterolateral edge there is an elongate prominence which articulated with the vestigial first metatarsal.

Metatarsals: The vestigial first metatarsal is roughly oval and flat in posteromedial view, with a raised area on the lateral end of the anterior side. It bridged the gap between the lateral edge of the entocuneiform and the back of the head of the third metatarsal, articulating with the latter by a large facet. The contact with the entocuneiform left no facet.

Only the proximal ends of the second, third, and fourth metatarsals are preserved. The configuration of their proximal facets complements that of the distal facets of the distal tarsals (see Fig. 21) and need not be described here.

The pes of *Tapirus* (see Figs. 19–22) differs from that of *Heptodon* in the following features: astragalus relatively lower and wider, lacking a flange on the distal end of the lateral side of the trochlea; astragalo-navicular and astragalo-cuboid articulations relatively shorter (anteroposteriorly) and wider, and the latter more horizontal; proximal astragalo-calcaneal articulation shallower, with a lower proximal face; distal astragalo-calcaneal facet relatively higher and bent slightly; calcaneum lacking a pit above the proximal calcaneal-astragalar facet for the fibula, and with a
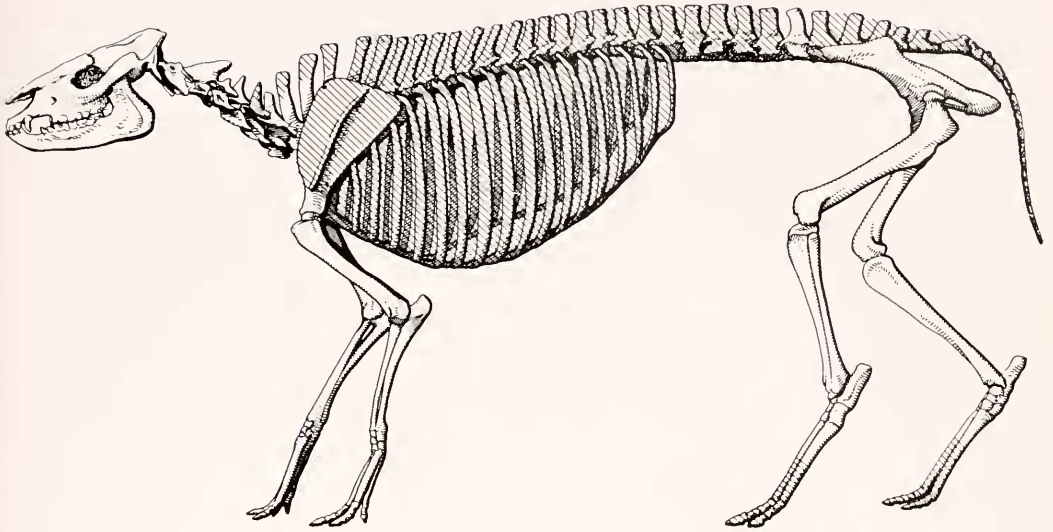
Fig. 23. *Heptodon posticus.* MCZ 17670. Skeleton in lateral view to show general proportions. Restored portions indicated by hatching. Slightly less than ¼ size.

much shallower pit for the short lateral ligament; calcaneo-cuboid articulation relatively narrower; no calcaneo-navicular contact; cuboid relatively lower and longer (anteroposteriorly); anterior cuboid-navicular contact relatively larger; articulation between cuboid and fourth metatarsal more saddle-shaped and less flat; navicular relatively lower; ectocuneiform relatively lower and wider, without the small proximal posterior tuberosity seen in *Heptodon*; ectocuneiform-mesocuneiform articulation relatively smaller; mesocuneiform relatively lower and narrower, lacking a small proximal posterior tuberosity; entocuneiform more elongate. Metatarsals presumably relatively shorter and wider.

The differences listed above result in a relatively lower and wider tarsus in *Tapirus*, presumably in correlation with its heavier weight, compared to *Heptodon*. The absence of a pit on the calcaneum to receive the fibula in extreme flexion, and the lack of a flange on the astragalus for the fibula in extreme extension, suggests that a lesser degree of extension and flexion occurs at the tibiotarsal joint in *Tapirus* than it did in *Heptodon*.

CONCLUSIONS

The most striking osteological changes which occurred during fifty million years of evolution from *Heptodon* to *Tapirus* are modifications of the skull correlated with development of a proboscis. Primary changes were a tremendous enlargement of the nasal incision and a shortening of the nasals. These, in turn, caused several secondary changes. There were also less drastic cranial modifications which resulted from dental and brain evolution. By the end of the Oligocene, over 25 million years ago, the evolutionary changes which resulted in the modern tapirid skull were essentially completed, and there has been little cranial evolution in the Tapiridae since then.

The postcranial skeleton of *Tapirus* has remained basically similar to that of *Heptodon*, and most of the differences observed are correlated with the larger size of *Tapirus*. These differences include relatively broader and more robust limb bones and vertebrae, a less flexible vertebral column, and a much more expanded iliac blade in *Tapirus*.

Apparently, at some point in evolution

from *Heptodon* to *Tapirus*, there was a trend toward increasing cursorial specialization. This is indicated by such features in *Tapirus* as the reduction of the acromion of the scapula (correlated with loss of the clavicle), a widened lateral condyle on the humerus, the fusion of radius and ulna, and a relatively wider and shorter radio-carpal articulation than in *Heptodon*. However, modern tapirs are relatively heavy-bodied and short-legged, which suggests a more recent emphasis on large size, rather than speed, for defense against predators.

It is significant that the cursorial modifications mentioned above are confined to the fore limb; the same is true in other tapiroid lineages descended from *Heptodon*. This fact suggests that the hind limb of *Heptodon* was more specialized than the fore limb and had in fact approached its biomechanical limit of specialization for running (except for lengthening of distal limb segments in some tapiroid lineages). Thus, further modifications for running would be more likely to appear in the less specialized front limb.

ABBREVIATIONS

A	astragalus
aac	anterior opening of alisphenoid canal
alf	anterior lacerate foramen
C	cuneiform
Ca	calcaneum
Cu	cuboid
Ec	ectocuneiform
ef	ethmoid foramen
En	entocuneiform
feo	fenestra ovalis
fo	foramen ovale
fr	fenestra rotunda
ga	groove for artery
gav	groove for auricular branch of vagus
gct	groove for chorda tympani
gfn	groove for facial nerve
hf	hypoglossal foramen
iof	infraorbital foramen
L	lunar
M	magnum
Me	mesocuneiform
mf	maxillary foramen
mlf	middle lacerate foramen
N	navicular
of	optic foramen
ofc	opening of facial canal
P	pisiform
pac	posterior opening of alisphenoid canal
pgf	postglenoid foramen
plf	posterior lacerate foramen
pp	paroccipital process
ppf	posterior palatine foramen
ptp	post-tympanic process
R	radius
S	scaphoid
scf	sinus canal foramen
sf	stylomastoid foramen
spf	sphenopalatine foramen
T	trapezoid
Tm	trapezium
tt	ventral edge of tegmen tympani
ty	tympanic
U	unciform
Ul	ulna
I–V	metapodials

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Plate 1. *Heptodon posticus.* MCZ 17670. Lateral view of skull and mandible. Slightly less than natural size.
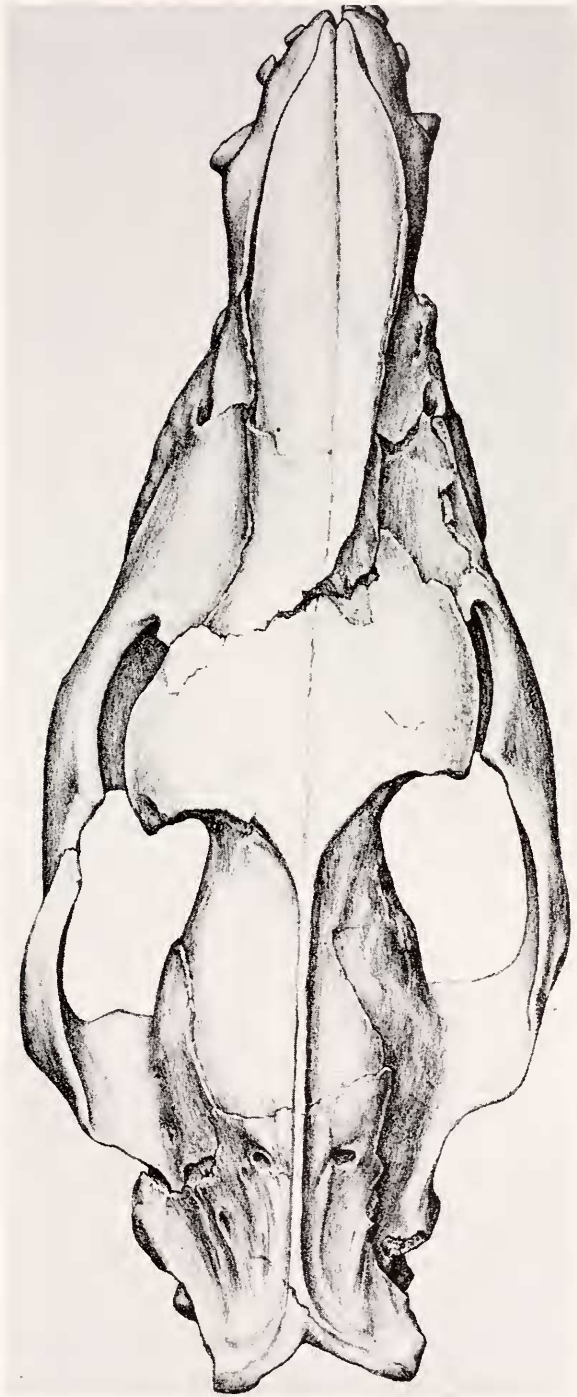
Plate 2. *Heptodon posticus*. MCZ 17670. Dorsal view of skull. Slightly less than natural size.
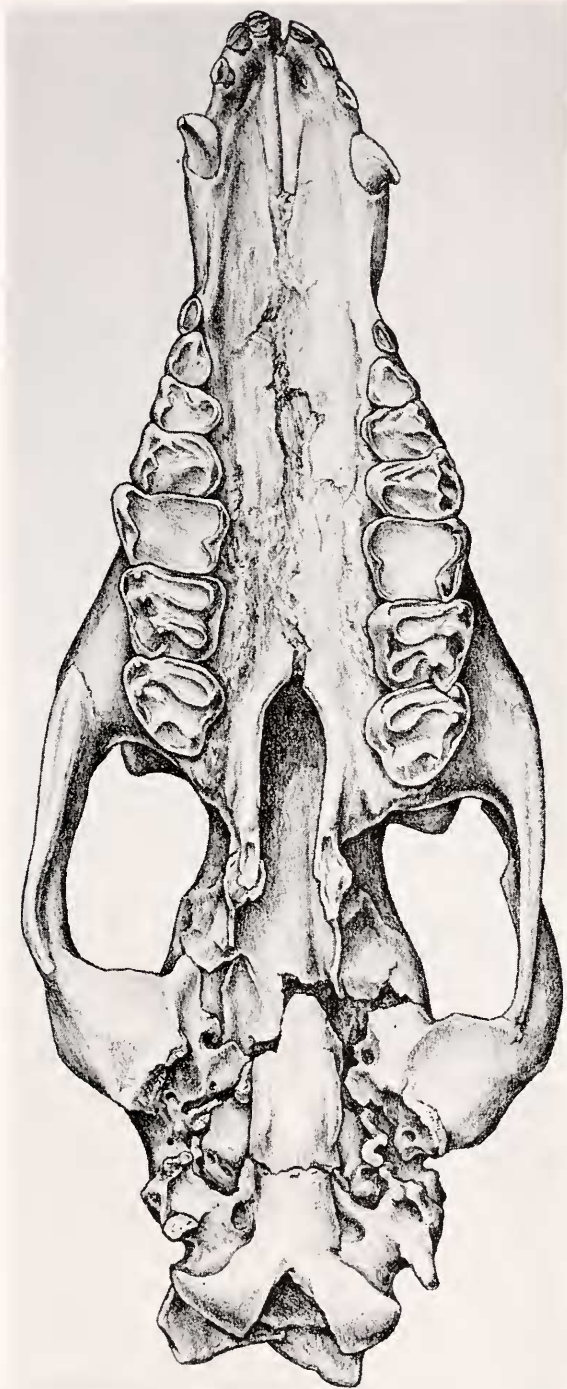
Plate 3. *Heptodon posticus.* MCZ 17670. Ventral view of skull. Slightly less than natural size.